HERBERTIA

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HERBERTIA

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Cover Photo: *Griffinia liboniana*. Photo by William Reuter.

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As a member of the INTERNATIONAL BULB SOCIETY you will receive the following yearly benefits:

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HERBERTIA VOLUME 54, 1999

EDITOR'S NOTES

Welcome to the 1999 volume of HERBERTIA, albeit arriving in the year 2000. The International Bulb Society has a new board, geographically diverse; a new publication (Bulbs), a magnificent presence on the Internet (www.bulbsociety.org), thanks largely to Web Director Kelly Irvin, and the aegis of a great history behind it. HERBERTIA remains the Society's great link to the past, and its unbroken span of 54 volumes, despite some name changes (and reversions) along the way, is well known for its contributions to botany and horticulture. It is an honor to continue this tradition and shepherd the flagship of IBS into the millennium.

We were deeply saddened in 1999 by the loss of Fred Meyer, who helped lead IBS during transitional times, and was lauded worldwide as a plantsman nonpareil. Fred posthumously shares this year's William Herbert Medal honors with Dr. Peter Goldblatt, whose contributions to our understanding of the Iridaceae are legion. A congratulation to contributor Veronica M. Read, UK National Collection Holder for *Hippeastrum*, who recently was awarded an RHS Gold Medal for her display of Hadeco South African hippeastrums at the RHS Westminster Show, London, United Kingdom.

As in volumes past, this issue of HERBERTIA contains a diversity of articles about geophytic plants, and a generous supply of accompanying color figures. Maintaining the standard of color graphic support for the articles in HERBERTIA is costly for IBS, but considered essential for maintaining the quality of the journal. The Board of Directors is thus extremely grateful for the contributions that have been made towards the Society's publication color fund.

Recommencing a tradition that past editor R. Mitchell Beauchamp started in the 1980's, a selected bibliography of geophyte scientific literature appears in Herbertia volume 54. To make up for past absences, this edition covers the years 1995 to 1999. We plan for this to be a regular feature of the journal.

Please note that the final deadline for submissions for volume 55 (2000) of HERBERTIA is September 1, 2000. This will allow both careful review of submitted articles, and a return to a normal publication schedule. Submission guidelines have been updated (they appear in this issue) and careful attention to format is appreciated. We will strive to have the next issue in everyone's mailbox before the REAL start of the third millenium!

ERRATA, Volume 53 (1998)

P. 38: Figs. 15, 16 should have been captioned *Rhodophiala bagnoldii* and *Rhodophiala advena*, respectively.

P. 47: Captions for Figs. 13 and 14 were transposed.

—Alan W. Meerow, Editor

In Memorium, Fred Meyer, 1953–1999

The following are personal recollections of Fred Meyer from some his many friends and colleagues around the globe.

Randy Baldwin, San Marcos Growers, Santa Barbara, California:
"It is hard to know the names of all who knew Fred as he had many friends but I am sure that anyone involved in horticulture at least knew of him. Fred was responsible for introducing or bringing to our attention so many plants and I am sure I only know a fraction of them.

"My own involvement with Fred began in 1980 when he introduced me to the many Proteaceous plants and Kangaroo paws that he was growing in his foothill ranch here in Santa Barbara. We became friends and worked together on a cut flower venture and on the Board of Directors for the Santa Barbara Horticultural Society and Friends of Franceschi. During this time he arranged with sources of new plants for annual plant sales for the Horticultural Society from people such a Merv Turner (Bush Gem Kangaroo Paws) and Rodger Elliot and shared generously from his own collections of bulbs, Aloes and Coral Trees. On a trip north he introduced me to M. Nevin Smith's Wintergreen Nursery and the fledgling UCSC arboretum where he encouraged me to purchase and trial many new plants that still grow today.

"In 1983 he imported a collection of hybrid New Zealand Flax from Margaret Jones that we planted in a field at San Marcos Growers; this group of plants has since become signature plants for our nursery. And of course the *Alstroemeria!* I think every nursery is still growing a Meyer's hybrid *Alstroemeria* of some form. His more recent work with *Hippeastrum, Calibrichoe* and *Petunia* was something. I know Fred was excited about and I hope that those working with him on this see fit to immortalize him in the names of the plants. This just the plant side of Fred—as a friend he introduced me to new foods, restaurants, ideas and things I will only remember as time goes on. We have lost a great horticulturist, plant breeder, and I have lost a friend."

Ehrentraud Bayer, botanist, Munich Botanical Garden, Germany:
"I was totally shocked when I heard the bad news about Fred. It is a long time ago that I met him first in California on a 'Herbertia-Congress' and it is years ago that we met in Munich but I remember him very well. I also remember very well how he enjoyed staying in Munich and going to a typi-

cal Munich beer-garden. I still have in mind the picture of Fred sitting at the table taking beer and Bavarian food and looking happy. I would have liked him to be with us another time."

R. Mitchel Beauchamp, horticulturist and environmental consultant; former executive director of the International Bulb Society:
"The selection of plant materials beneficial to mankind has been achieved by only a special, small group of individuals. The legacy of Robert Fortune, David Fairchild, F. H. Wilson, George Forrest, F. Kingdon Ward, Paul Hutchison and Howard Scott Gentry is well chronicled. These people developed a strong base for our horticultural and economic botany industries today. Among these late, great plantsmen must now be placed my friend, Fred Meyer. Fred had a lot of ideas on how to develop new and wonderful plant cultivars. He has left us a legacy as a reminder of his gift to horticulture. Our lives are much greater because of him."

Julie Dutilh, taxonomic botanist, Brazil:
"I met Fred in 1988, when he came to a floriculture meeting in Campinas, Brazil. As I had just finished my thesis about taxonomy and cytology of Brazilian *Hippeastrum* species, he came to see the collection at the Agronomic Institute.

"That was when we started to talk about *Hippeastrum* and other geophytes. It was the first time I had someone else who liked them as much as I did, and who knew so much about them! For all those years since we kept in contact, he helped me very much with bibliography, plant material, a lot of advice. We made several trips together, in the US and especially in Brazil, to see plants (not just geophytes), and to keep on discussing about them. His intelligence and knowledge of genetics and breeding was stimulating. It was such a support to me, he helped me get over several low periods in my life.

"And it was not just the plants. I got to know a very warm person, with so much interest in everything that was happening around him, in the people that surrounded him. When he came to Brazil he used to spend some time at my house and he built a friendship with my husband and two daughters, who also liked him very much. We also were very warmly received at his house when we went to California, and once he treated us to a beautiful trip by car from San Diego to San Francisco, along the coast.

"It was a blessing, for me and my family, that we were able to spend his last Christmas together. We stayed for a week in a small town in the middle of Brazil, at the border of a National Park. It is a very beautiful place, very

quiet, and some species of *Hippeastrum* I had told him about were flowering. He was so pleased to see them, and there were so many other beautiful plants in flower that delighted him, besides the animals and the surroundings. It was really a very special holiday, we all felt very close and were able to talk so much about so many things. His warmth will always be felt."

***Rodger Elliot, Australian plantsman and author of* The Encyclopedia of Australian Plants:**
"His contribution to professional and amateur horticulture and floriculture was phenomenal and his memory will live on in these areas because of his contact with so many people and for all those different plants he made available to people. I can always remember my first visit to Fred's family home and one of the first things that Fred asked me was if I could sign Volume One of the Encyclopedia. 'Sure,' I said. He then proceeded to bring to me a copy that was nearly worn out through constant use. The pages were not quite falling out but in some cases were extremely close to doing just that! It was indeed very touching and heartening for a writer that somebody could put one of your books to such fantastic use."

Rob Griesbach, research geneticist, U.S. National Arboretum, U.S. Department of Agriculture:
"Fred and I worked together for over a decade on plant breeding. I will never forget his Friday morning phone calls where we discussed a lot more than our cooperative research. We talked about everything from species with untapped economical potential to new methods in molecular taxonomy. Fred was a wealth of information and never stopped asking questions. His appetite for learning was unbelievable. Besides being a great researcher, he was a silent benefactor to many. He gave freely of his time, talents and money. He will be fondly remembered as both a great friend and researcher."

Harold Koopwitz, University of California Professor; former director, UCI Arboretum and author:
"Fred Meyer was as close to a genius as anyone I ever met associated with the plant world. He had a phenomenal appetite for information about plants and an amazing ability to recall that information. This was combined with a boundless enthusiasm and great energy to get things done. Fred was a resource, if there was something about plants one needed to know, he was the man, either giving you the information instantly or helping locate it. Fred was the modern global man with a web of international friends and ties.

"I knew him for more than two decades and during that time we worked closely on several projects. He had a keen interest in the activities of the UCI Arboretum and kept a close watch on our work in endangered bulbous plants. He funded a collecting expedition to Chile and helped financially with several other projects. We had a joint project on breeding *Ornithogalum*, and in a four year period accomplished the equivalent of 12 years breeding work. We also collaborated very closely on an enormous gladiolus breeding program incorporating genes from wild species into the newest modern hybrids. Multicolored, scented and thin-stemmed cut flower gladiolus resulted and some of these have now been introduced into the trade. He had an exceptional mind and with it goes the potential for exciting new flowers and plants that only he could perceive and create. Horticulture will be the poorer for his going."

Alan W. Meerow, research geneticist and systematist, Germplasm Resources, U. S. Department of Agriculture, and author:
"While I will miss my colleague Fred Meyer—his brilliance, genius, and myriad accomplishments as a plant scientist—, the truest loss is that of a friend whose generosity, warmth, and spirit has enriched my life for almost two decades. The Monday Morning Meyer phone call became an institution that started my workweek, the expectation of which still haunts me in an unguarded moment. Fred and I were so different, yet just as equally kindred souls. We argued, got frustrated with each other at times, but our bond never weakened."

A. Fernando C. Tombolato, floriculturist, Agronomic Institute of São Paulo, Campinas, Brazil:
"Fred and I traveled a lot together. He always helped me a lot to be together making observations on wild plants and learning a lot about them. I will be always very thankful to Fred about this. I had the chance to be with him many times of my life for my birthday and he always wanted to go to a very nice restaurant where we spent a really good time tasting new flavors and talking about special meals. Fred was a gourmet, and I knew a lot about fine food because I lived in France for four years in Bordeaux, place of good wines and close to Gascogne, the land of the *foie gras*. Fred also liked to cook, but the only chance we had to cook together was last January, when he came to Brazil. One day our old friend, Luiz Matthes, who was, in the past, the Head of the Floriculture Department of the Instituto Agronômico where I currently work, invited us for dinner at his house. Fred liked the idea so much that he decided

to prepare the menu himself; the only thing he asked for from Luiz was two ducks. We bought the other things in a very fine supermarket in Campinas, where we live. We had a nice evening together, everybody firstly in the kitchen, then in the dining room, and finally in the living room for coffee. The most interesting thing we learnt after the dinner was that the ducks which Luiz bought were very expensive because they where imported from Canada. Fred couldn't stop laughing when he heard that, and he said to me many times, 'When I am back in the U.S., I need to find a wild Canadian duck postcard to send to Luiz! He will feel great!' That´s about Fred´s very fine sense of humor. Those who were very close to him can understand and remember so many similar occasions. Fred was a very good fellow and knew how to enjoy every moment, with or without money."

A Eulogy for Fred Meyer, delivered by Angus Stewart at a memorial mass: "There can be no greater privilege in life than to meet people of the stature of Fred Meyer. Such opportunities come but once in a lifetime. Fred was so many things to so many people, and to each and every one of them he was a guiding light, a teacher and an inspiration. His life was devoted in equal measures to his family, friends and his beloved flowers. He was a person who rose above the humdrum of everyday existence and, through the enormous strength of his character achieved more in his life than most of us can ever dream of.

"Fred will always be remembered for his great love of family and friends. All of us have benefited from his unrivaled generosity of spirit, his wonderful sense of humor, his booming laughter and above all the inspiration and enthusiasm that he brought to our lives. Children especially were the recipients of these gifts and he developed an instant connection with them.

"All of us who worked with Fred found it impossible to separate work and pleasure, for that is what Fred's work was to him. It was a passion that soared to remarkable heights. The truly remarkable quality of his work was its holistic nature. Without any formal training in plant sciences Fred was able to not only understand, but also take to new heights our understanding of areas as diverse as botany, plant conservation, genetics and breeding, plant physiology and plant collecting. His stage was truly the world in his work. He was known and highly regarded on every continent where he was equally welcomed and respected in both the scientific and commercial world. He could more than match wits with experts in any of the fields he chose to apply his talents to. The path to Fred's door was well worn by many

of the world's most respected scientists and plant breeders who regularly sought his counsel and inspiration.

"Fred's work in ornamental plant breeding will ensure that he will live on in the best possible way. We will all be able to treasure Fred's spirit as we nurture and admire the sublime beauty of his unique creations. Fred's love of art and the finer things that the human spirit can produce was appreciated by those who knew him. Indeed, Fred's own artistic creativity is embodied in his plants and they will live on as works of art that rival any canvas or sculpture. Far better than those static works of art, Fred's plants will be multiplied and propagated to be enjoyed by people all over the world for generations to come. Fred's love of the finer things in life is no better demonstrated than in his successful quest to introduce the new dimension of fragrance into commercial varieties of *Gladiolus* and *Alstroemeria*.

"Fred loved the challenge and discovery of plant collecting around the world. Fred was a free spirit who delighted in his eclectic adventures on every continent whether it be collecting *Hippeastrum* in Brazil, *Limonium* in the Mediterranean, red and green kangaroo paws in Badgingara, Western Australia or tuberose in his beloved Mexico. It was in this capacity that he taught himself botany, to the point where he discovered and described species new to science. His philanthropy in this area was legendary as he fulfilled what he saw as his responsibility to record and pass on his knowledge to the scientific community. In particular he had a passion for the flora of South America, and Brazil and he has been instrumental in encouraging research in this area of the world. He often commented on the satisfaction it brought to him to see the jobs created by his breeding work in developing countries.

"Some measure of the scope of his work can be gathered by the list of plants with which he has bred. This includes *Alstroemeria*, tuberose, *Hippeastrum*, *Petunia*, *Gladiolus*, *Limonium*, *Ornithogalum* and kangaroo paw. Even though his work has been and will continue to be influential worldwide, Fred was extremely modest and always sought to give others credit where it was due. His generosity in this regard fostered co-operation and positive outcomes in all his projects around the world.

"Our lives have been immeasurably enriched by knowing Fred Meyer. Fred's star has burned brightly and intensely and now he has left us, well before his time was due. He has, however, left us the richest of legacies that will forever inspire us to realize the true potential of the human spirit.

"Farewell Fred."

THE HERBERT MEDAL

The Herbert Medal is the highest honor that the International Bulb Society can bestow upon a person for meritorious achievement in advancing the knowledge of bulbous plants. The medal is named for William Herbert (1778-1847), son of Henry Herbert, Earl of Carnarvon. William Herbert had a predilection for amaryllids and achieved success in their hybridization. He published his research findings in several monumental works. His contributions as a pioneer geneticist and plant breeder, and his arrangement of the Amaryllidaceae, helped set the stage upon which other workers, both amateur and professional, have been able to advance.

The award includes honorary life membership in the Society.

The Herbert Medal may be awarded annually or on special occasions by the Board of Directors of the Society. Medalists need not be members of the Society to be considered for the Herbert Medal.

PAST HERBERT MEDALISTS

Mr. Henry P. Nehrling, Florida, 1937
Mr. Theodore L. Mead, Florida, 1937
Mr. Arthington Worsley, England, 1937
Mr. Ernst H. Krelage, Holland, 1938
Mr. Cecil Houdyshel, California, 1938
Maj. Albert Pam, England, 1938
Mr. Pierre S. duPont, Delaware, 1938
Mr. Jan de Graff, Oregon, 1938
Mr. Fred H. Howard, California, 1939
Mr. Sydney Percy-Lancaster, India, 1939
Dr. J. Hutchinson, England, 1939
Mr. Carl Purdy, California, 1939
Dr. A. B. Stout, New York, 1939
Mr. H. W. Pugsley, England, 1940
Mr. W. M. James, California, 1941
Prof. Dr A. Fernandes, Portugal, 1942
Miss. E. Lawrence, North Carolina, 1943
Dr. Henry A. Jones, Maryland, 1944
Mr. R. G. Huey, Kentucky, 1945
Mr. Guy L. Wilson, Northern Ireland, 1946
Mr. R. W. Wheeler, Florida, 1947
Dr. R. A. Dyer, South Africa, 1948
Capt. C. O. Fairbairn, Australia, 1949
Mrs. Mary G. Henry, Pennsylvania, 1950
M. Mulford B. Foster, Florida, 1951
Dr. J. C. Th. Uphof, Florida, 1952
Mr. E. A. Bowles, England, 1953
Mr. Thomas R. Manley, Pennsylvania, 1954
Dr. Robert F. Hoover, California, 1955
Mr. E. O. Orpet, California, 1956
Mrs. Morris W. Clint, Texas, 1957
Mr. Wyndham Hayward, Florida, 1958
Dr. Robert G. Thornburgh, California, 1959
Prof. Ira S. Nelson, Louisiana, 1960
Mr. Frederick B. Jones, Texas, 1961
Dr. Floyd F. Smith, Maryland, 1962
Mr. W. D. Morton, Jr, Louisiana, 1963
Mr. S. Y. Caldwell, Tennessee, 1964
Mr. Robert D. Goedert, Florida, 1965
Mr. L. Boshoff-Mostert, South Africa, 1966
Dr. Marton Cardenas Hermosa, Bolivia, 1967
Dr. Robert P. Kahn, Maryland, 1968
Mr. W. Quinn Buck, California, 1969
Dr. Thad M. Howard, Texas, 1970
Dr. C. G. Ruppel, Argentina, 1971
Mr. J. L. Doran, California, 1972
Dr. Cesar Vargas, Peru, 1973
Sr. Pierfelice Ravenna, Chile 1974
Dr. John M. Cage, California, 1975
Mr. Floor Barnhoorn, South Africa, 1976
Mrs. Emma D. Menninger, California, 1977
Dr. W. S. Flory, Jr., North Carolina, 1978
Mr. Harry Blossfeld, Brazil, 1979
Mr. Charles D. Cothran, California, 1980
Mr. W. L. Tjaden, England, 1981
Walter & Hilda Latapie, Louisiana, 1982
Mrs. A. C. Pickard. Texas, 1982
Mrs. Marcia C. Wilson, Texas, 1983
Dr. Hamilton P. Traub, California, 1985
Dr. Thomas W. Whitaker, California, 1988
Mr. Grant E. Mitsch, Oregon, 1988
Mr. L. S. Hannibal, California, 1988
Dr. H. Shuichi Hirao, Japan, 1990
Dr. Kenneth E. Mann, California, 1991
Mr. Brian Mathew, England, 1992
Dr. Maurice Boussard, France, 1996
Sir Peter Smithers, Switzerland, 1997
Dr. Dierdre Snijman, South Africa, 1997
Dr. Alan W. Meerow, Florida, U.S.A. 1998

1999 Herbert Medalist
Peter Goldblatt

Peter Goldblatt is the Curator of African Botany at the Missouri Botanical Garden, St. Louis, Missouri with which he has been associated since 1972, when he left a teaching position at the University of Cape Town, South Africa. Goldblatt has made the study of the iris family a lifetime research interest and he is one of the world's leading experts on the Iridaceae and its close relatives. Although members of the Iridaceae are worldwide in distribution, the family has marked concentration on the African continent where over 1000 of the estimated 1800 species are native. His research on various genera of the Iridaceae has taken him on numerous field trips to Africa as well as southern Europe, the Middle East, and parts of North America. His travels in the field have been funded by the U.S. National Foundation and the U.S. National Geographic Society. Author of some 200 scientific papers, Goldblatt has also written several botanical monographs including *The Moraeas of Southern Africa* (Kirstenbosch Botanic Garden, 1986), *The Genus Watsonia* (Kirstenbosch Botanic Garden, 1989), *The Woody Iridaceae* (Timber Press, 1993), *Gladiolus in Tropical Africa* (Timber Press, 1996) and most recently *Gladiolus in Southern Africa* in collaboration with John Manning (Fernwood Press, 1998)

Autobiographical Notes

Born and reared in Johannesburg, in what was then the Transvaal, South Africa, I studied botany and zoology at the University of the Witwatersrand, in Johannesburg. After graduating there in 1966 with a B.Sc. degree, I taught undergraduate courses in botany for a year, before assuming a teaching position at the University of Cape Town. At the same time I began graduate study for a Ph.D. degree. The unusual flora of the Cape Region of southern Africa with its rich and diverse flora of bulbous plants always fascinated me and even as a child I had maintained a living collection of native bulbous plants. In Cape Town I was conveniently placed for a study of the chromosome cytology and morphological research in the *Iris* family, Iridaceae, that became the subject of my dissertation.

Despite a fair teaching load during the following four years, I completed my dissertation in 1970 under the guidance of Professor E. A. Schlepe and graduated in 1971. I was fortunate in having Professor Robert Ornduff, of the University of California, Berkeley, as an external examiner, largely because he happened to be in South Africa for a year's sabbatical leave at the time that I completed my dissertation. That connection essentially made it possible for me to get a temporary position at the Missouri Botanical Garden in 1972 for the purpose of studying the systematics of a group of poppy species in the Middle East. The Missouri Botanical Garden had hired the energetic Peter H. Raven as director the previous year, and under his tutelage the garden prospered and began to expand. My project on *Papaver* was a direct result of his obtaining a contract from the U. S. Department of Agriculture to study the systematics of drug-yielding poppies as part of a broader undertaking to identify and domesticate alternative sources of morphine-type alkaloids (generally known as opium in the raw state, and the source of the addictive and illegal drug heroin). Until then, the sole source of opium was the widely cultivated *P. somniferum*. That project resulted in the discovery of populations of one of the oriental poppy species that yielded unusually high concentrations of pure alkaloid that could not be easily converted to heroin and seemed to be a solution to the heroin addiction explosion in the early 1970s.

With the completion of my role in the project, I was offered a permanent position at the garden as curator of African botany, a position endowed in 1975 by the late B. A. Krukoff, a botanical benefactor who believed that a U.S. institution should maintain a research interest in the African flora. The Missouri Botanical Garden thus became *de facto* the center in North America for African botany with me holding the endowed chair of B. A. Krukoff Curator of African Botany. As result, the garden actively sought to expand its herbarium collections of African plants and its library holdings of literature relating to the African flora. At the same time that I was responsible for expanding the African collection there, Peter Raven encourage me to return to my original research interest in the African bulbous flora. The Iridaceae, with more than 1200 species in sub-Saharan Africa, became the focus of my botanical research. With grant support from the National Science Foundation, I undertook a series of revisionary studies of African genera, beginning in 1974 in *Moraea* and *Dietes*, and continuing in 1976 with *Galaxia*, *Gyanndriris*, *Homeria*, and *Hexaglottis*. These genera all belong in subfamily Iridoideae and are related to the northern hemisphere genus *Iris*.

After publishing revisions of these genera I turned my attention to subfamily Ixioideae, largest of the four subfamilies of the Iridaceae, containing some 950 of the estimated 1800 species in the family. Additional grants from the National Science Foundation made it possible for me to conduct extensive field work, first on *Freesia*, obviously because of its importance in horticulture, and later on *Geissorrhiza* and *Hesperantha*, large genera that had not been studied in recent times. As a result the number of new species waiting to be described was quite amazing, at least for southern Africa where the flora had been studied for more than 20 years. I was to eventually describe over 40 species in these two genera, about one-quarter of the species now recognized. The genus *Watsonia* was an even greater challenge because of the complications resulting from hybridization in disturbed habitats in parts of its range. That study made it possible to publish a monograph of this very attractive genus, one that has tremendous horticultural potential. Many of the native species are cultivated in southern Africa, and in California, Australia and New Zealand where the climate is similar.

During fieldwork in Africa over a 12 year period, I maintained my early interest in *Moraea* and in the process discovered several additional species, rendering my earlier work, published in scientific journals, somewhat incomplete. I then decided to try to produce a book on the genus that would incorporate the new species in a coherent account of this large genus. With the collaboration of the artists Fay Anderson and Margo Branch, and the support of Kirstenbosch Botanic Gardens, the lavishly illustrated book, *The Moraeas of Southern Africa*, was published in 1986.

A particularly interesting group of African Iridaceae is the woody genera, *Klattia*, *Nivenia*, and *Witsenia*. Although comprising just 14 species, it proved a daunting group of plants to investigate. These plants are true shrubs with woody stems and an evergreen habit, thus are most unusual members of an otherwise largely bulbous plant family. Detailed study of seed development, anatomy, and inflorescence morphology confirmed that, despite their unusual growth form, they are fairly specialized members of the family. The woody irids represented an unusual challenge for me because they are mostly montane plants with small ranges that grow in isolated places across the western and southern mountain belt of South Africa. Fortunately, I was able to enlist the help of the legendary South African botanist, Elsie Esterhuysen, a pioneer in the study of the southern African mountain flora. Then more than 70 years old, she nevertheless led me to inaccessible sites where many of the woody irids grow, taking me along

trails I never knew existed. Research on the woody irids gave me my first brush with reproductive and pollination biology, a field I was to investigate in depth in the following years. Some of the woody irids are heterostylous, a condition unique in the family and a fairly rare condition in plants, and their pollination is fairly diverse, involving birds, large bees, and long-proboscid flies. Work on the woody irids culminated in the publication of 1993 by U.S. publisher, Timber Press, of *The Woody Iridaceae*, a work also illustrated with drawings by Margo Branch and watercolors by Fay Anderson.

One glaring gap in our knowledge of the Iridaceae of Africa was a lack of understanding of the systematics of *Gladiolus* in tropical Africa. An account of the genus for the region, published in 1898, was virtually meaningless in the late 20th century. However, there were huge herbarium holdings of *Gladiolus* in major European and African herbaria. With field work in parts of Africa where that was possible combined with examination of thousands of herbarium collections, it became clear that *Gladiolus* is, in fact, a major genus in tropical Africa, where there are some 82 species. Many currently recognized names had to be synonymized but that was more than offset by the recognition of more than 20 new species, and the inclusion of *Acidanthera* and *Oenostachys* with their several species in *Gladiolus*. The results of my research on *Gladiolus* were published by Timber Press in 1996 in *Gladiolus in Tropical Africa*, a book illustrated with photographs and a series of line drawings by John Manning, a South African botanist and gifted artist.

A close connection between the Missouri Botanical Garden and the Museum National d'Histoire Naturel in Paris made it possible to me to work as a visiting scientist there in the late 1980's and early 1990's. I became familiar with the floras of francophone Africa and of Madagascar as a result and was able to produce floristic accounts of the Iridaceae of Madagascar and Cameroon, and fundamentally improve my understanding of the Iridaceae. Working in Paris I was able to collaborate with Annick Le Thomas, a palynologist of worldwide renown. Together we explored the variation in pollen characteristics in the irids, discovering in the process the importance of pollen in understanding the phylogeny of the family, notably the distinctive operculum of the ixioids. Our work also produced a major step forward in understanding the genus *Aristea*, which, though lacking distinctive flowers, has more variation in its pollen than the rest of the family put together. That discovery led to the reclassification of *Aristea*, an important Afro-Madagascan genus of the Iridaceae. The comparative success I had in producing illustrated botanical accounts of attractive genera led me to under-

take my largest botanical project, a study of *Gladiolus* in southern Africa, the center of the genus in terms of its diversity and number of species. With what I thought would include some 120 species, this was a large undertaking. I enlisted the collaboration of John Manning, with whom I had been working on a study of seed development as well as the pollination biology of *Lapeirousia*, and who had provided drawings used to illustrate *Gladiolus in Tropical Africa*. In 1991 we thought the undertaking was timely because of a revision of southern African *Gladiolus* by the late G. J. Lewis published in 1972. It was out of print and outdated after only 20-odd years owing to the sinking *of Anomalesia, Homoglossum, Kentrosiphon,* and *Oenostachys* in *Gladiolus,* plus the addition of several new species. Because of its horticultural importance we decided to aim for a definitive account with generous illustration. We invited the artists Fay Anderson and Auriol Batten to provide watercolor paintings and promised to obtain living material for them to work from. As we began to search out species across the subcontinent, the scale of what we had undertaken dawned on us. We quickly found the taxonomy was incorrect in some instances and that there were also several new species in southern African herbaria. By the time we had finished our research in 1997, we recognized 163 species of *Gladiolus* just in southern Africa. And our doughty artists had painted 144 of them, an admirable achievement. It took John and I more than 6 years of field work, largely funded by the National Geographic Society, as well as drawing, writing and painting to complete the work. With the financial support of several organizations, notably the Stanley Smith Horticultural Trust and First National Bank of South Africa, *Gladiolus in Southern Africa* was published in 1998.

While John and I were studying *Gladiolus*, we also found time to undertake a series of studies of pollination biology. The impetus for thus work was the discovery that many African Iridaceae have specialized pollination systems, something quite unusual on a world scale. Many species actually are dependent on just one organism for their pollination and hence seed production. Prominent among these specialized pollinators are long-proboscid flies belonging to the horsefly and tangleveined fly families. These flies have probosces usually well over an inch long and sometimes more than two inches long and feed primarily on the nectar of a series of plants with elongate floral tubes. Prominent among such plants are many irids, mainly in the genera *Gladiolus, Hesperantha,* and *Lapeirousia.*
Understanding of pollination biology was a revelation to us and we quickly came to understand the adaptive importance of floral form, color, and

marking in the African flora. This of course led us to a better understanding of the patterns of variation in the flowers of the Iridaceae, and it became an important factor in our systematic work on *Gladiolus*, which we integrated into our monograph.

Apart from my work on the African Iridaceae, repeated visits to Africa made me aware of the unusual flora there, especially in the Cape region, an area of winter rainfall and summer drought. That climate plus fairly unusual soils and isolation from the rest of Africa by semideserts left the flora of the Cape region to evolve in relative isolation. Thus it came to have a suite of plant families, genera, and species that are highly distinctive, so much so that the flora is recognized as just one of six floral kingdoms in the world. I found myself in the happy position of being able to collaborate with Pauline Bond, who then worked at Kirstenbosch Botanic Gardens in Cape Town. On an account of the flora, something until then unavailable and desperately needed for a multitude of purposes, not least for conservation of this tiny, but botanically unique part of the world. *Plants of the Cape Flora*, published in 1982, had an immediate and positive effect. Ecological studies of many different kinds were now possible and conservation projects finally made real progress. The book was, for a floristic account, a real success, and was out of print 10 years later when a revised volume was commissioned by the South African National Botanical Institute. I agreed to participate in producing a revised treatment of the Cape Flora, little realizing that without the energetic collaboration of Pauline Bond, who had retired, I had taken on more that I could handle. John Manning, also now working at Kirstenbosch, quickly filled Pauline Bond's role. Working closely with him, we enlisted the participation of several South African botanists in producing a revised account of the Cape Flora, substantially improved in descriptive content, taxonomy, and distributional information. The new volume, *Cape Flora*, now in press, recognized 9000 species in this tiny part of the world, almost 70% of which are endemic there. Among these plants are the world's greatest concentration of bulbous plants. Some 15% of the flora are plants with bulbs, corms, or similar underground organs. These include more than 650 species of Iridaceae, almost 200 species of Hyacinthaceae, nearly 100 species of Amaryllidaceae, and many Colchicaceae, Hyposidaceae, and Haemodoraceae. This bulbous flora is the subject of a book that John Manning, Dee Snijman, and I are preparing for publication by Timber Press.

This personal account of my career in botany would be incomplete without an expression of thanks to the many people with whom I have collaborat-

ed and to the several botanical institutions that have hosted my field and laboratory work. Personal interaction makes for more enjoyable and invariably more productive work and more insightful results. I also owe Peter Raven and the Missouri Botanical Garden an enormous debt of gratitude for encouraging me to follow my natural interests and enthusiasm for the work I have wanted to do and for smoothing the way when difficulties arose. Funding agencies, especially the National Science Foundation and the National Geographic Society, made much of my fieldwork possible. I am hugely grateful to these institutions, as I am to the Stanley Smith Horticultural Trust for awarding grants to help publish my books, thus making them accessible to the world at large and not just to the scientific community.

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1999 Herbert Medalist
Fred Meyer

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Biographical Notes

There are rare individuals that are born with a genius and a passion that determines their life's work. Such was the case with Fred Meyer. Fred was born December 6, 1953 in Upland, California and was tending his first garden at the age of three. He was born to Estella, of Mexican origin, and La Vern Meyer, of German extraction originally. Fred's relatives on both sides of the family gave him a very interesting and unique cultural perspective on the world. This cultural mix was to blend with all the unique and exciting influences that California had to offer the young man through the 60's and 70's. Wherever Fred lived during his formative years he would make a point of seeking out whatever flowers were in the vicinity. Perhaps the remarkable atmosphere of California in the 1960's also had a profound influence on his character and love of flowers.

During the early 60's, the Meyer family moved to the "Valley of Steinbeck," the Salinas Valley. There they lived in a ranch house surrounded by acres of plum and prune orchards. The profusion of blossoms every spring was an inspiration to Fred and no doubt helped to develop his passion for the large-scale commercialization of plants. It became apparent to those close to him in his family that this eye for commercializing little known plants was a unique talent that should be nurtured.

In the mid-sixties the family moved to Escondido where re-established his relationship with his maternal grandmother. They worked closely in her garden, where the Mexican influence in Fred's life was extended and enhanced. His interest in things Mexican would continue throughout his life, not only the flora, but the cuisine, architecture and art as well.

Towards the end of the decade the family moved to Valley Center, five miles east of Escondido, and Fred built his first greenhouse with the help of his paternal grandfather. The greenhouse was used for breeding *Cattleya* orchids as well as starting a seedling project with conifer trees for Christmas tree production.

By the early seventies Fred had graduated from Escondido High School. It was typical of Fred's amazing passion for obscure groups of plants that at this stage of his life he had amassed the world's best collection of *Erythrina* species (Coral trees) which he subsequently donated to Waimea Garden in Kaimea, Hawaii. It was also during this period that Fred's unique ability with plants became abundantly clear to his family and plant friends.

He was accumulating not only a collection of plants but also botanical and horticultural books from around the world that contributed to his encyclopedic knowledge. His photographic memory enabled him to absorb phenomenal amounts of information about a plant's habitat, horticulture, breeding patterns, etc. For any given plant, Fred could construct a holistic picture of it in his mind that enabled him to predict how to grow and breed with it.

After graduating from high school, Fred was faced with trying to find a career that would allow him to express his extraordinary and unique talents in the plant world. He started at Palomar College, where he studied agricultural engineering. Meanwhile the family had moved to a new property that was to become known as the Hidden Meadows Ranch. Fred encouraged the move, one of the reasons being the unique architectural style of the house. Architecture was one of Fred's many interests, which also included cooking, art collecting and an appreciation for an eclectic range of music from Beethoven to the Beach Boys. Fred cajoled and convinced his father Vern to plant rare and unusual members of the Proteaceae from South Africa and Australia, plants that were at that time regarded as very exotic. The Hidden Meadows Ranch would become very important, as it served as a conference room for Fred, within the confines of which he hosted luminaries of the horticultural and botanical universe from around the world. He would live there with his parents and family, on and off, until the end of his life.

By the mid seventies Fred was planting out the ranch at Hidden Meadows. During this period he would meet and be influenced by many prominent people in the plant world including Howard Asper Jr., flower growers William and Linda Teague, Howard Scott Gentry, Rude? Middleman, and Paul Hutchinson of Tropic World Nursery in Escondido. Most of Fred's important influences were from California and he typified the dynamic energy of this unique state. Fred was in his element with brother Thom, driving

the back roads of California listening to old Beach Boys' tapes while hunting for *Brodiaea*, *Godetia* or whatever genus of plants was their current fancy. Fred was a fun-loving person whose sunny disposition was reflected by his ready smile and booming laugh. He was the quintessential Californian.

During this period Fred initiated collections that were to become life-long interests. He was avidly collecting a huge range of South American and Australian plants with *Hippeastrum* being a particular focus at this time. Fred's work with *Hippeastrum* was to continue for the rest of his life, and his new cultivars are currently re-writing the judging books in bulb shows in the Netherlands. During this period Fred moved to San Luis Obispo where he continued to study agricultural engineering, but he soon felt that college classes were irrelevant to him at that point, thus he quit academic life. It would be fair to say that there was no college or university on earth that could have been able to match Fred's self-tuition in his chosen vocation.

In 1975, he persuaded his father to buy over 1600 acres in the foothills of Santa Barbara ("Rancho Vista del Mundo") where he would establish an enormous collection of Australian and South African plants and begin his tremendous work with bulbs from every continent. Fred moved to Santa Barbara and planted out 20 acres of proteas and other floral exotics, as well as orchards of cherimoya and avocado on 100 acres. Fred's interests in the South African Proteaceae led him to start a breeding and selection program in *Leucospermum* (Pincushions). The results of this program were used to provide new material for the Meyer cut flower operation.

Throughout the seventies the "Fred Meyer Collection" of bulbous and bulb-like materials grew at an exponential rate as Fred started to rapidly build a network of world-wide contacts. This collection included dozens of genera from all over the planet, and was used as a resource not only for Fred's breeding programs, but others all over the world. Fred's interest in plants had philanthropic overtones, as he felt a responsibility to distribute his material to whoever needed it, whether botanist, amateur collector, breeder, or plant conservationist. Typical of his generosity was his involvement with various public gardens. Around 1978 Fred was donating Australian plants to assist in the landscaping of the Los Angeles Zoo. He also began an association with Huntington Gardens to which he donated and helped plant many of the specimens in the Australian section of the garden. During this period of his life he started breeding euphorbias, aloes, cacti, proteas, and *Anigozanthos*. Hybrids of this era can still be found in the gardens at Hidden Meadows ranch and other private gardens.

In the late seventies Fred started his association with the International Bulb Society (then, the American Plant Life Society) as well as with leading plant breeders around the world. Fred was also working actively in the cut flower industry at this time and was building an extensive reputation as an innovator and developer of new crops. He worked very closely with Jan Oudendijk, an import broker in Holland, and from this period on he and his brother Thom developed an extraordinary partnership in cut flowers and plants.

Fred and Thom were inseparable in the plant business until the time of his death. Thom provided his brother with support in many ways and this helped enable Fred to achieve the highest level in his endeavors. In turn, Fred inspired Thom to educate himself and establish his own plant interests. The hallmark of the work of these two brothers was to search for, select and breed plants that could be adapted to the cut flower industry. In doing so they continually broke new ground as Fred traveled around the world seeking out new material.

During the period from 1978–1981, Fred had started a huge collection of Californian native plants. His keen eye for wild material and its potential for ornamental horticulture drove this collection. Bulbous plants such as *Brodiaea* and annuals such as *Godetia* and *Eustoma* were all collected and sent to breeders in Holland, Israel and Japan for various commercial breeding programs.

Fred traveled to Australia in 1980 to collect plants in Victoria and Western Australia. It was on this trip that he met Rodger and Gwen Elliot, both prolific authors on Australian plants as well as keen propagators (Rodger is co-author of the world-renowned Encyclopedia of Australian Plants). This meeting began a collaboration that was to result in a huge range of rare and unusual Australian plants being introduced by Fred through Rodger and Gwen. On this trip Fred traveled extensively in Western Australia and was particularly fascinated by the Stirling Ranges with all its wonderfully exotic endemic members of the Proteaceae and Myrtaceae in particular. He would also seek out members of the scientific community such as Dr. Jennifer McComb who was developing in vitro propagation techniques for kangaroo paw propagation. Fred would return to California with an excellent collection of all sorts of rare and wonderful Australian species that he would introduce to the cut flower trade. His father Vern was particularly captivated by Fred's prized acquisition *Verticordia grandis*, the scarlet feather flower, which he was convinced would light a fire under the cut flower industry in California.

The early eighties saw Fred gaining confidence in respect to his contacts with the scientific community. At this time he would meet one of the most influential persons in his life, Professor Abraham Halevy, the great plantsman

and plant physiologist based at the Hebrew University in Jerusalem, Israel. He would encourage Fred to believe in himself as a self-taught horticulturist who was the equal of any professional in his chosen field of endeavor. This relationship began a period of intense cooperation that was to last for the rest of his life with Israel's leaders in floriculture such as Danziger Nursery and various breeders at the Volcani Institute. Fred would provide germplasm of wild species of many genera to these breeders. In the early 1980's Fred also began a long-standing relationship with various members of the U.S. Dept of Agriculture's Floral and Nursery Plant Research Group at Beltsville, Maryland. His colleagues there included Roger Lawson, Rob Greisbach and Mark Roh. On many occasions Fred donated or raised funds to support the work of the Research Group and he was highly respected there as a source of inspiration for new projects. Around this time Fred began a long-standing friendship with Japanese plant breeder Kaz Sato of the Dai-Ichi Seed Company. Sato was the breeder of the famous *Limonium* Misty series. Fred's work with Sato involved supplying germplasm of all sorts of plants for Dai-Ichi's breeding programs. In the mid-1990's Fred undertook an extensive collecting trip to Spain and Morocco collecting wild limoniums for Dai-Ichi. This material will be the basis for many new commercial statice hybrids of the future. Fred was fascinated by the science of plant breeding and naturally gravitated towards the leaders in the field worldwide whose respect he quickly gained and they found in him a generous and willing contributor. It is hard to estimate the part he has played in changing the direction of ornamental plant breeding around the world but there can be no doubt that his influence was profound.

In 1982 he organized and funded an expedition to collect in Peru, Ecuador and Chile. The primary purpose was to find new *Hippeastrum* to introduce novel characteristics for this genus into his breeding program, and his return from South America precipitated another frenzied period of breeding activity in this group.

During this period also, his influence and good will would be shown again by his assistance to people such as Randy Baldwin, who would later establish San Marcos Growers, one of the Santa Barbara area's most notable nurseries. Noted California horticulturist Steve Brigham was another associate during this period. Fred's influence was to inspire and assist with propagation material to introduce new plants, particularly Australian material, to the nursery trade. His work with the nursery trade was merely a hobby, for it was the cut flower industry that remained the focus of his work. Through his amazing

library and collection of scientific literature Fred was teaching himself plant physiology, taxonomy, breeding and propagation to the point where he could hold his own with the experts in these disciplines from around the world.

In 1984 Fred sponsored a trip with Thad Howard and Dylan Hannon to collect tuberose relatives for his breeding project with *Polianthes* (Agavaceae). His objective was to introduce a range of color into new tuberose cultivars. He was highly successful in his objective and the world will marvel in the not too distant future at his vision for this delightful group of plants as his new cultivars are released.

In the mid-eighties Fred started a close association with the University of California Irvine Arboretum. Fred's philanthropy to the arboretum was remarkable as he donated substantial amounts of money for greenhouses and plant collecting expeditions and publications associated with plant taxonomy and conservation. Fred worked closely during this period with Professor Harold Koopowitz. Koopowitz recalls: "For many years he was an active worker on the Board of the Friends of the UCI Arboretum. He was also on the board for the International Bulb Society, during a difficult time in that organization's life, and even arranged and paid for one issue of the society journal, *Herbertia*. A few weeks before his death we had a long phone conversation. We discussed some of our past activities and we both decided that the International Conference on Bulbous and Cormous Plants, held at the University by the UCI Arboretum and International Bulb Society in 1989, would probably go down as the highlight of our careers. Somehow we were able to bring conservation biologists, plant scientists, commercial bulb growers and serious amateurs together and get it all to work smoothly. Much of the kudos for this rests with Fred, not only was he very generous in financial matters but he also worked tirelessly to make the conference the great success that it was."

At the International Conference on Bulbous and Cormous Plants, Fred met various people who would become influential in his work. One of these was Jiming Huang, a Chinese researcher in floriculture from Shanghai. Fred would travel to China to lecture and collect. Fred was instrumental in finding Jiming a job in the United States with Ball Seed Company. This was typical of his generosity in fostering the careers of the many friends he made in the plant world.

Fred's gladiolus project was typical of his approach during this period of his life. What began as a study on Fred's part to clarify relationships between different *Gladiolus* species ended up as a remarkable breeding project that yielded many unique cultivars that have excited commercial interest around

the world. Fred assembled an extensive collection of glad species, including some of the rarest and most interesting. Harold Koopowitz, Fred's collaborator on this project, recalls: "We incorporated genes from wild species into the newest modern hybrids. Multicolored, scented and thin-stemmed cut flower gladiolus resulted and some of these have now been introduced into the trade."

Fred's interest in the taxonomy of the Amayllidaceae led to friendship and professional association beginning in the mid-1980's with Alan Meerow, former University of Florida professor and now a research scientist with the U. S. Department of Agriculture. Meerow was a graduate student at that time, working on the systematics of the Andean members of the family, and he and Fred exchanged large amounts of plant material from their respective collecting trips to South America. When Meerow began his professorship with the University of Florida in 1987, and undertook a *Hippeastrum* breeding program of his own, this exchange continued in the form of pollen and offset bulbs of amaryllis species and hybrids.

By 1986 Fred had moved back to Escondido from Santa Barbara and his work from then on was centered at the Hidden Meadows Ranch. Fred formed a company with Thom and two other partners called Vista Wholesale Florist. This once again demonstrated Fred's commitment to commercial floriculture. He would serve as president for 5 years and, until his death, was a shareholder and member of the Board of Directors.

Through his interest in the cut flower trade, Fred initiated work on a huge range of plants. An extensive *Alstroemeria* breeding program created some superb long-blooming tetraploid cultivars. A recently released, highly heat-tolerant cultivar called 'Las Olas', developed with Alan Meerow, is typical of his work in this genus.

A trip to Israel was undertaken in this period to work with Professor Halevy and his colleagues. Through his contacts there he would introduce new cut flower varieties of sunflower to the U.S. In return Fred would collect and supply breeders in Israel with wild sunflower species which would be incorporated into their breeding programs. This work was typical of many other projects he was doing at the time with breeding companies all round the world. New *Achillea* cultivars from Holland, *Craspedia* from Australia, hybrid Anemones from Israel are a few examples of his introductions during this period. Fred's uncanny ability to turn his hand to any genus and grow it commercially was one of his most amazing qualities. These new lines were introduced to the commercial world through Vista Wholesale.

The scope and potential of his breeding work led Fred, Thom and sister Marlene to establish New World Plants Inc, as the commercial vehicle for the marketing of Fred's new plants. As part of this enterprise Fred established a plant tissue culture laboratory at the Hidden Meadows Ranch under the guidance of Australian horticulturist Angus Stewart. The laboratory was the catalyst for Fred to enter the emerging field of biotechnology, particularly its application to plant breeding. Fred would utilize in vitro techniques such as embryo culture, mutation breeding with colchicine and meristem culture to eliminate viruses. The lab was also extensively used to initiate cultures of Fred's new plants to be sent to companies around the world. Typical of Fred's newfound interest in tissue culture techniques was a range of *Limonium sinuatum* cultivars he selected for delicate pastel colors and minimal stem winging. These cultivars formed a group known as 'Pastel Magic', and they were popular in the cut flower trade in the late eighties. The laboratory continues to this day to be managed by Fred's sister Marlene. Both Marlene and Thom became intimately involved in Fred's work as a result of New World Plants and it is fair to say that both have played a major role in enabling Fred to achieve at the highest level. Fred's frequent trips meant required that someone be at home "holding the fort".

In the late 1980's, Fred, together with Alan Meerow, began a fruitful and close relationship with two Brazilian colleagues, Julie Dutilh, a taxonomic botanist, and Fernando Tombolato, a horticultural researcher. This relationship involved several expeditions to South America and Brazil in particular. They collected a huge range of species from *Alstroemeria* to Petunia, *Hippeastrum* and many others. Fred became a familiar visitor to this part of the world where he fostered the work of these scientists monetarily and academically. As with all his associates around the world his relationships quickly grew beyond plants and he established close friendships with both Fernando and Julie.

Alan Meerow reminisces about the many weeks he spent in the field with Fred, Julie and Fernando: "We always managed to turn heads in the small towns of the Brazilian interior, three men and one woman, two gringos and two *brasileiros*, arriving late in the hours of dusk, sweaty and filthy after a long day collecting. Fred was so unselfconscious wherever we went, always easy-going, and acting naturally. After finding accommodations, the next priority was always to locate the best restaurant in town. Good food, good wine, and good fellowship; how Fred's eyes shown under those circumstances. He would turn to me and say, " Is this great, or what?" The four of us would spend hours together laughing, teasing each other unmercifully, but always getting

the job done, too. We had to laugh, knowing full-well we would be spending hours that night cleaning plants in the hotel room's sink and commode!"

Throughout the nineties Fred continued to breed and introduce many new plants. He returned to *Alstroemeria* and collected many new species in Brazil with his colleagues. These were used in a breeding project in Colombia to develop heat tolerance. This project was done in conjunction with Camilo Herrera of Jardines de los Andes in Bogota and Fernando Tombolato of Instituto Agronomico de Campinas in Brazil.

He was also working with Dai-Ichi in Japan, Angus Stewart and S. & P. Dominello in Australia, Ball Seed Co in the U.S. and Perchei-Hatabor in Israel for the release of his winter flowering gladioli. Leo Berbee & Sons began the exciting task of introducing Fred's amaryllis to the European market. He was working closely with Danziger Nursery in Israel on several projects, and had been arranging shipments of plants from them only hours before his untimely death.

Yet another example of Fred's philanthropy was his remarkable contribution to the publication of botanist Peter Goldblatt's book *Gladiolus of Tropical Africa*. This was a botanical book detailing the various little known gladioli of Central Africa. When it became obvious that there were insufficient funds to publish the book with full color illustrations, Fred orchestrated an international campaign among his commercial associates to raise the necessary funds. Rather than receive money for the rights to his new gladioli hybrids, Fred asked that money instead be donated to the publication of Goldblatt's book.

In 1995 Fred traveled through Spain and Morocco collecting wild limoniums for Dai-Ichi's breeding program. This trip typified his many expeditions, as he first combed the scientific literature for the localities of the various species, and then systematically retrieved them. His vision will influence the future breeding of this important floral crop for decades to come.

One of his last major trips took place in 1996 when Fred traveled to Australia to deliver a paper at the International Society for Horticultural Science Symposium on new crops for floriculture. He was accompanied by Fernando Tombolato, and Australian horticulturist and writer Angus Stewart. Fred's ability to identify obscure and unusual plants constantly amazed his companions. Even more incredible was the fact that he had cultivated many of these plants at home in Escondido. Kangaroo paw breeder Angus Stewart tells a story that adequately sums up Fred's genius:

"I had long been interested in a variant of the spectacular red and green kangaroo paw (*Anigozanthos manglesii*), the floral emblem of Western Australia. This variant is a subspecies, *A. manglesii* subsp. *quadrans*, which has a multi-branched flower stem unlike the subsp. *manglesii* with its unbranched stem. On being presented with information, Fred instantly recognized it from his trip some 20 years earlier. He then proceeded to lead us on a journey through the back blocks of Badgingarra for many miles along isolated dirt roads. He then pulled up at a solitary group of the desired plant in the middle of nowhere and gave us his characteristically modest shrug of the shoulders followed by a wonderful smile as he stepped out of the car to enjoy his find. The form he located had up to 8 branches, a characteristic that will be invaluable in developing new and spectacular red and green hybrids in the future."

Fred Meyer died of natural causes on the 12th of May, 1999 at the age of 45.

Thom and Marlene Meyer are committed through New World Plants, Inc to commercializing Fred's breeding work as a living legacy of his career and accomplishments.

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The Ecology and Cultivation of Rare and Little-Studied Ledebourias in Southern Africa

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The taxonomy of the genus *Ledebouria* was in a state of some confusion until its revision by Mr Stefanus Venter for his MSc thesis. In the period since this remarkable piece of research was submitted to the University of Natal in 1993, some of the new species discovered by Venter have been formally described, while others are still in the process of publication. Other, apparently new, species have been found and further research needs to be conducted on these plants to determine their taxonomic status in the genus. The discussion that follows concerns several rare and little-studied species, some of which have unpublished names, but will be published in due course.

The species studied are found in two distinctive habitats: rocky grassland and shallow, sandy soil at the edges of sheets of exposed rock. The latter habitat is very specialized and rarely colonized by other vegetation, except the numerous grasses that are the dominant vegetation type in most hillside habitats of the summer rainfall area of South Africa.

Ledebourias that compete with grasses for light and growing space usually produce all their foliage and complete flowering in the spring and early summer months. They flower best after veld fires have cleared the grassland in the winter months, which are May to August.

Species frequenting shallow soil over sheets of exposed rock flower from September to December. Those from the high rainfall areas flower mostly in September and October, whereas species from the more arid areas only come to full growth and flower once the main summer rains start in November and December.

A number of South Africa bulbous plants are adapted to seasonal inundation and this applies to several *Ledebouria* species, particularly those which grow in sandy soil over sheets of exposed rock.

One of the most extreme forms of *Ledebouria* ecology is encountered in *L. monophylla* (Venter in ed.). This species grows in dense mountaintop grassland and scrubland, which may be burnt rather rarely, perhaps once every six years or more. Flowering takes place only in the two years following veld fires, before the plants are crowded out by dense vegetation. This interesting ecology is discussed below.

Ledebouria seed is very fertile and generally germinates in large numbers soon after it has been set, provided there is sufficient moisture. The exceptions to this general rule are species found in more arid areas with erratic rainfall, such as *L. viscosa*.

ECOLOGY OF GRASSLAND AND SCRUBLAND LEDEBOURIA

Two populations of *L. monophylla* were studied: one, a very large and extensive population in the mountains of the Mount Sheba Nature reserve in Mpumulanga and another, much smaller population in the short dense grassland on the summit of Mount Anderson, also in Mpumulanga.

Research on the Mt. Sheba population was first conducted in January 1998. At this time the mountain slopes were covered in tall grass and scrub, the latter often in dense stands 1–2 meters high, beneath which the ground was covered in carpets of fallen leaves. The only *L monophylla* that could be found were growing on exposed cuttings at the edges of the hiking trails that criss-cross the mountainside.

A severe fire occurred during the winter of 1998, burning all the vegetation off he mountainside. After the first substantial rains in October there followed one of the most spectacular floral displays of *L. monophylla* ever witnessed at this locality. All mature bulbs bloomed in late October and early November. An abundant seed set followed this display. The debris from the fire and the soft soil loosened by the rainfall resulted in ideal germinating conditions. Large dense groups of seedlings were visible everywhere around the groups of adult bulbs. During the late summer months the regeneration of the scrubland had begun and some groups of *L. monophylla* were already well screened from the sun.

The population on Mount Anderson is much smaller. At the time the research was conducted (November 1998), the grassland had not been burnt except for a firebreak along the perimeter of the colony that is burnt annually. Very few plants in the rocky grassland had flowered but most of those in the firebreak area had bloomed and were in seed. The population here was also much larger, clearly benefiting from the regular burning.

Fire evidently plays a critical role in the regeneration of *L. monophylla* populations. For mass germination of seeds, it seems that the importance of fire lies not only in opening up the habitat, but also in the soft debris it leaves behind. The larger the intervals between fires, the greater the accumulation of this debris and the soft pockets of soil conducive to abundant germination.

One of the rarest *Ledebourias* frequenting mountaintop grassland is *L. rupestris*. To date this species has only been recorded from the vicinity of the

Macmac Falls in Mpumulanga, where it grows in short mossy grassland around exposed sheets of rock. This plant is one of the few *Ledebouria* species adapted to growing in dense moss as well as sandy pockets amongst the rock. *L. rupestris* flowers very early in September and is usually in seed by early October, which is the beginning of the rainy season. The habitat of this mountain-top species is cleared mostly by winter drought that shrivels the mosses and sparse grass cover amongst which the species grows. Early flowering and seeding insures that, despite their limited size, these plants are able to compete successfully with the surrounding cover. *L. rupestris* is one of the few species that often germinates in dense moss. The young bulbs grow in the moss for a few years before penetrating and lodging in the soil below.

The *L .rupestris* populations at the MacMac falls are currently threatened with extinction. A building development now occupies the site of the largest population and local vendors of clay pots use clumps of moss in which are growing *L. rupestris* bulbs to decorate their containers. Fortunately the species is easily grown from seed produced in cultivation and these stocks could be used to satisfy horticultural demand and reintroduce plants to suitable habitat.

One of the most interesting and rarest of ledebourias is confined to hills in the vicinity of Grahamstown in the Eastern Cape. *L. hypoxidoides* (Fig. 1) has very attractive leaves similar to those of *Hypoxis* but even more pubescent . Dense, scrubby vegetation and grass (Fig. 2) covers their typical habitat, much of which has diminished through suburban development and reforestation with exotics. Even in relatively pristine areas the plants are never very numerous, usually occurring singly or else in small groups of 2–5 plants. Little opportunity is afforded for expansion as the cover is too dense and the plants are confined mostly to exposed rocky areas where the grass and scrub growth sparsest (Fig. 3).

A very interesting phenomenon has occurred at one of the colonies studied on the eastern outskirts of Grahamstown. The plants have formed large concentrations on an abandoned sports field. At this site they are very common, with so many seedlings that they grow in tiers in certain parts of the field. In the natural hilly habitat behind the field (Fig.1) the plants are, as elsewhere, thinly and sparsely distributed. The colonisation of the sports-field is a clear indication how *L. hypoxidoides* is able to proliferate in a habitat where there is little competition from scrub and grasses.

Ledebouria minima (Fig.4) is one of the smallest species in the genus. It is usually rather sparse and local, particularly when it grows in hilly grassland with a dense herb and grass cover. One of its strongholds is the western section of Gauteng near Carletonvillle, an area with a large number of gold

Fig. 1.

Fig. 1. (left) A fine specimen of *L. hypoxidoides*, showing the unusual pubescent leaves. This plant is one of a large colony flourishing on an abandoned sportsfield outside Grahamstown.

Fig. 2. (above) The rocky hills around Grahamstown are home to *L. hypoxidoides*. Plants are sparsely distributed in their natural habitat on the hillside in the foreground, but have proliferated on the abandoned sportsfield below.

Fig. 3. Sparse scatterings of parent plants and seedlings display the typical distribution of *L. hypoxidoides* in their natural habitat.

Fig. 4. *Ledebouria minima* is one of the smallest species, with mature plants little more than 8cm across, and is found typically in these shallow sandy pockets and washes. One plant may produce several flower stems in one season as this specimen shows.

Fig. 5. In years of burning, seeds of *L. minima* are able to lodge in grass tufts and germinate and grow. They may however only bloom when fire has cleared the grass.

Fig. 6. *Ledebouria confusa* in bloom in a typical damp and shallow niche. The packed bulb scales which protect it from veld fires are clearly visible.

Fig. 7.

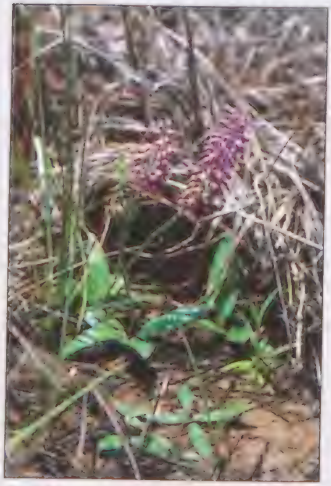

Fig. 8.

Fig. 7. Winter fires sweep across the hills of Cullinan in Gauteng nearly every year and plants are adapted to cope with this phenomenon. The rough black stems of *Xerophyta retinervis*, which covers the hillsides, are well insulated by packed layers of old leaf bases, while the bulbs of *Ledebouria confusa* are similarly protected by a dense layer of bulb scales.

Fig. 8. *L. lepida* also grows in the surrounding grassland but is much more sparsely distributed. In years when veld fires clear the grass, it is able to seed itself successfully in the smallest of open patches, as may be seen from the number of young plants around this mature specimen in flower.

Fig. 9. *Ledebouria lepida* is one of several species adapted to growing in the shallow soil at the edges of exposed rock , where conditions may range from very dry to very wet. The tiny plants (from 3cm to 6cm across) may be seen here growing across the entire wet area.

Fig. 10. A parent plant of *L .lepida* in fruit surrounded by a brood of youngsters.

Fig. 11. The unusual foliage and flowers of the dwarf ledebourias is best enjoyed in pot cultivation where they make highly decorative subjects. Pictured is *L. galpinii*.

Fig. 12. *Ledebouria hypoxidoides.*

All photographs by Laurian Brown.

mines. It is a haven for several rare plants, particularly asclepiads and aloes. *L. minima* grows on south-facing hill slopes, usually in shallow sandy soil at the edges of sheets of exposed rock. Here the grass cover is the shortest and least dense, but the species is also thinly scattered throughout the surrounding grassland. Flowering occurs in October and early November once the main summer rains have begun. As with other *Ledebouria* species, flowering is particularly good after grass fires (Fig. 5), followed by abundant seed set. *L. minima* is one of the few *Ledebouria* species that may go dormant well in advance of the autumn, often in February or early March.

THE ECOLOGY OF LEDEBOURIAS IN SHALLOW SOIL ON AND AT THE EDGES OF SHEETS OF EXPOSED ROCK

Shallow soil on, and at the edges of, sheets of exposed rock is a singular niche exploited by several bulbous and caudiciform species. The habitat is subject to a number of extremes, particularly temperature, but also moisture. Competition for niches in which plants can grow is not nearly as intense as that in the surrounding grassland.

Ledebourias that have evolved to exploit this niche are not necessarily confined to it alone; many of them occur also in rocky areas with sparse cover in the surrounding grassland. Three examples are *L. confusa*, (Venter in ed), *L. cooperi*, *L. lepida* (Venter in ed.) and *L. saundersonii*. *L. confusa* and *L. lepida* are rather rare species, whereas the other two are familiar and widespread, particularly *L. cooperi*, which is very common at certain localities.

Ledebouria confusa and *L. lepida* display two interesting adaptations in growth and flowering habits to conditions that range periodically from very dry to very wet. *L. confusa* is one of the few ledebourias with a bulb often exposed well above the ground. It escapes desiccation with numerous tightly packed bulb scales which also protect the bulb from fire (Fig. 6).

Flowering and seeding takes place at the beginning of the main summer rains in late October and early November. Flowering is particularly good after fires when the rocky hillsides on which the plants grow are barren for the first few months of early summer.

The recruitment of young plants to the populations is particularly successful at this time. Seeds are buried in dust and burnt plant material that retains water for several days after a thundershower. This allows seeds to germinate in shallow soil over sheets of exposed rock, a situation which would otherwise be too dry were it not for the addition of new soft porous material from burning.

Ledebouria confusa is currently known from two isolated populations: one on the sheets of exposed rock in the southern foothills of the Waterberg north of Nylstroom in the Northern Province, and the other in very rocky hills near Cullinan in Gauteng (Fig. 7). The latter colony is particularly large and impressive and provides excellent opportunities for the study of this fascinating species.

The bright lavender flowers of *L. lepida* (Fig. 8) make it one of the most spectacular of the dwarf species. It occurs in sandy soil over sheets of sandstone and is currently known from grassland on the summit of the Waterberg to the southeast of Vaalwater in the Northern Province (Fig. 9).

Ledebouria lepida is fully dormant until the main summer rains in mid-November. Once the sand in which the plants grow is fully saturated, the bulbs begin to emerge from dormancy. The soil may remain wet for weeks on end. Flowering usually coincides with the months of highest rainfall, in December and early January. The plants produce copious amounts of seed in late January and early February. The seeds germinate within a few days after it is deposited on the wet sand around the parent plants. With very little competition in this particular niche, some of the colonies become very dense (Figs. 9 & 10.)

Ledebouria lepida is also found in much smaller numbers in the surrounding grassland. (Fig. 7). Here it competes directly with grasses and is only able to flower and set seed significantly in years when winter grass fires have cleared the habitat.

Ledebouria cooperi is particularly abundant in the Graskop area of Mpumulanga. The plants proliferate in seepage areas, particularly where there is shallow, peaty soil over sheets of exposed rock. In some area they form dense mats of many thousands of plants. This ideal habitat is saturated throughout the summer growing period and there is little competition from grasses that proliferate in the surrounding areas with deeper soil. There is also another significant factor behind this abundance. Much of the Graskop area is heavily forested with exotic pines. The remaining areas are unsuitable for stock farming and harbor very few indigenous antelope species. As a result, the L. *cooperi* populations are thinned neither by trampling or grazing. Moreover, most of the habitats are burnt each year as firebreaks between pine plantations. This creates ideal conditions for the annual flowering and seeding of this species year.

Ledebouria saundersonii (Venter 1993) is fairly widely distributed in mountainous grassland in Natal and Mpumulanga. It is regularly encountered on the Steenkampsberg in Mpumulanga, growing in wet situations over and

at the edges of sheets of exposed rock. The summit of this range is characterized by dense short grassland,. The only localities not colonized by grasses are the sandy areas occupied by *L. saundersonii*. Flowering in these mountains occurs in October and November once the main summer rains have begun. The germination pattern and general ecology is very similar to that of *L. lepida*, but the flowering time is earlier because the Steenkampsberg has very high rainfall, unlike the Waterberg where *L. lepida* is found.

CULTIVATION

All *Ledebouria* species discussed in this paper are easily cultivated. The ideal medium is one-third sandy soil, one-third fine seedling gravel, and one-third silt. The plants need to be kept dry during dormancy but watered regularly during the summer growing season. Some species from seepage areas, such as *L. cooperi*, perform best when they are kept constantly moist.

All ledebourias grow in direct sunlight and these conditions should be imitated in as far as possible in cultivation. Some species must be well watered only periodically if they originate from habitats that dry out between periods of rainfall. *L. confusa* and *L. hypoxidoides* are typical examples. If *L. hypoxidoides* is overwatered, the leaves lose their velvety appearance and flowering becomes erratic.

Ledebourias can be grown from seed with considerable success. We have found that most species in cultivation in Johannesburg set abundant seed and rarely seem to hybridize. The smaller species such *L. galpinii* (Fig. 11) are fully mature and ready to flower in their second season from seed. It is possible that many species could be cultivated out of doors in milder climates in the Northern Hemisphere, provided that they are not exposed to prolonged winter rainfall.

Dwarf ledebourias make very appealing rockery and container plants because of their striking foliage and flowers (Figs. 11, 12). Massing the bulbs in terracotta or stone pots and dressing the surface of the soil with appropriate natural gravel makes for an extremely attractive effect.

The hybridization and cultivar potential of ledebourias is, as yet, largely unexplored. There is little doubt that this provides local and international horticulturists with many opportunities.

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THE GENUS *GRIFFINIA* KER GAWLER (AMARYLLIDACEAE), REVISITED

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INTRODUCTION

Griffinia Ker Gawler is a small and critically endangered genus (Dean, 1995; Walter and Gillet, 1998) endemic to Brazil. The genus *Griffinia*, established in 1820 by Ker Gawler, was named in honor of Mr. Griffin, a botanist/horticulturist of South Lambeth, England. The type species for both the genus (Ker Gawler, 1820) and tribe Griffinieae (Ravenna, 1969a), *Griffinia hyacinthina* (Ker Gawl.) Ker Gawl., was originally referred to the genus *Amaryllis* L. (Ker Gawler, 1816). By the end of the Nineteenth Century, seven species of *Griffinia* had been described. The genus remained unaltered until the mid-Twentieth Century. In 1960, *G. rochae* Morel, a small-flowered *Griffinia* from the state of Rio de Janeiro, became the first new species in the genus described in almost one hundred years.

The most recent taxonomic treatment recognized six species (Traub and Moldenke, 1949). Since then, the monotypic genus *Hyline* Herbert, founded in 1841, has been reduced to a subgenus of *Griffinia* (Ravenna, 1969a), *Griffinia* subg. *Hyline* Rav., and one other species belonging to that subgenus was described. Additionally, five species belonging to the other subg., *Griffinia* subg. *Griffinia*, have been described (Morel, 1960, 1961; Ravenna, 1969c, 1974a, 1974d, 1978a; Preuss and Meerow, in press). In all, twelve species are currently recognized (Preuss, 1999).

GEOGRAPHIC DISTRIBUTION

Complete distribution patterns for the species of *Griffinia* are not yet fully known, but appear to be disjunct. The plants are now rarely found in the remnants of the Brazilian Atlantic Forest, or Mata Atlântica, estimated to have been reduced to less than 8% of its former range over the past 500 years. Populations of *Griffinia* are small, and occur as isolates in the remnants of the original vegetation of the Mata Atlântica (subg. *Griffinia*) and the dry *cerrado* and *caatinga* of the interior and the Northeast (subg. *Hyline*). Distribution patterns of both plants and animals in northeastern and eastern Brazil indicate the expansion of open vegetation formations (i.e. savannas, campos, cerradao, or caatingas) and accompanying forest contrac-

tions during the late Quaternary (Ledru, 1993). The expansion and contraction of various forests throughout the Quaternary, characterized by "great environmental instability", was responsible for speciation events for a large number of tropical taxa (Bigarella and de Andrade-Lima, 1982) and is likely to have influenced the evolution of *Griffinia* as well.

The state of Rio de Janeiro has yielded collections for the type specimens of *G. hyacinthina*, *G. ornata* Moore, *G. intermedia* Lind., *G. rochae* Morel, as well as the monotypic *Worsleya rayneri* (Hooker, f.) Traub and Moldenke, which DNA sequences indicate as the sister genus to *Griffinia* (Meerow et al., in press). Therefore, it is reasonable to presume that this state may have been a center of diversity (or origin) for the tribe and its two genera. The type localities for *G. aracensis* Rav., *G. itambensis* Rav., and *G. liboniana* Morren are from the state of Minas Gerais. These three type specimens are from single collections, and, with the exception of *G. liboniana*, collections from Minas Gerais have not since been reported. However, material referable to at least *G. aracensis* and *G. liboniana* has been collected from the state of Bahia (Preuss, 1999). *Griffinia parviflora* Ker Gawl. and *G. espiritensis* Rav. occur in Bahia and Espirito Santo to the south. Collections of *G. gardneriana* (Herb.) Rav. from Ceará and Maranhão, and *G. alba* Preuss and Meerow, from Pernambuco represent the northeastern limit of distribution for the genus. The distribution of *Griffinia* subg. *Hyline* (*G. gardneriana* and *G. nocturna*) is broad. Plants occur in seasonally dry regions, and collections have ranged from Mato Grosso do Sul, Tocantins, and Pará, to Bahia, Pernambuco, Maranhão, and Ceará.

MORPHOLOGY

The bulbs are tunicated and offset by production of daughter bulbs and/or bulbils from rhizomes, which appear root-like. The petiolate leaves range in form from elliptic to ovate, and are slightly falcate in subg. *Hyline*. The lamina, which has a distinct midrib, has pronounced parallel venation intersected by transverse striae, and may be variously speckled whitish in some species. The scape is solid, ancipitous (two-edged), and tumbling. The two spathe bracts are partially fused at the base and overlapping, persistent, and enclose a 2–20 flowered umbel of lilac and/or white zygomorphic flowers. The genus is unique in the Amaryllidaceae for the presence of a true hypanthium, formed by the continuation of the perigonal tube over the ovary in some of the species (Ravenna, 1969; Preuss, 1999). The positioning of the perigone is either epiperigynous (i.e. the floral tube surrounds the inferior ovary and forms a true hypanthium) or epigynous (i.e. the floral tube is

inserted at the top of the ovary). The filiform style is declinate and the stigma is capitate. The stamens are arranged in either a 5 + 1 manner (*Griffinia* subg. *Griffinia*) or all 6 fascicled and declinate (*Griffinia* subg. *Hyline*). The sixth stamen is sometimes obsolete in certain species of subg. *Griffinia*, but this character is not consistent. The fruit is an angular, ovoid, tri-loculicidal, dehiscent capsule, typically with one seed (Fig. 1). The seed lacks phytomelan, has a whitish testa, and is turgid and (sub-) globose (Fig. 2). The chromosome number for the genus is $2n = 20$ (Fig. 3), although $2n = 30$ occurs in some individuals (Preuss, 1999).

The morphology of the two subgenera is divergent, primarily in the flowers. In *Griffinia* subg. *Griffinia*, the leaves are symmetrical and vary from narrowly elliptic to broadly ovate. The lamina may be speckled whitish in some species (e.g. *G. liboniana* and *G. espiritensis*). The inflorescence is 4–20-flowered. The flowers are variable in size, ranging from 1.5 cm. to about 11 cm long, diurnal, unscented, and lilac and/or white. The perigonal tube is reduced in the small, blue-flowered species. The tepals are arranged in a 5 + 1 pattern, giving a bilabiate appearance. In the small epigynous species, the lowermost tepal is narrow, revolute and divaricate. Five stamens are declinate, and variable in length (two long and three short), and the sixth (when present) is assurgent. The pollen is white. The number of ovules per locule ranges from 2–10. The chromosome number is $2n = 20$ for most species, however, for some forms of *G. liboniana* and *G. espiritensis* the chromosome number is $2n = 30$, presumably triploid in origin. Most of these triploid individuals show reduced pollen fertility (Preuss, 1999).

In *Griffinia* subg. *Hyline* the leaves are slightly falcate and narrowly elliptic. The inflorescence is 2–3-flowered, and the flowers are large, nocturnal, scented, and white. The perigone is epiperigynous and fused into a tube, albeit highly variable in length. The perianth is not as strongly zygomorphic as in subgenus *Griffinia*. All six stamens are fascicled, in three ranks of two, and declinate. The pollen is yellow. The number of ovules per locule ranges from 10–16. In both species of the subgenus, the chromosome number is $2n = 20$ (Mookerjea, 1955; Preuss, 1999).

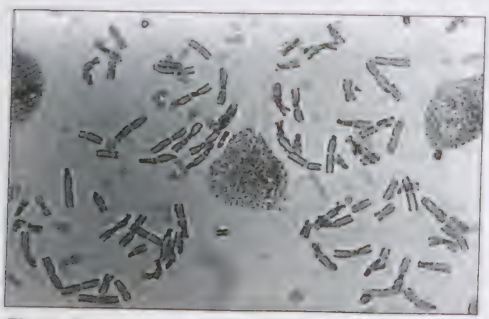

Fig. 3. Chromosomes of *Griffinia aracensis*. Four adjacent root tip cells undergoing mitosis; the chromosome number for this species is $2n = 20$.

PHYLOGENY/CLASSIFICATION

Based upon phylogenetic analysis of sequence data generated from the internal transcribed spacer regions (ITS) of nuclear ribosomal DNA (Meerow et al., 2000; Preuss, 1999) and also morphological characters (Preuss, 1999), a monophyletic tribe Griffinieae can be recognized. The tribe includes the monotypic sister genus *Worsleya*, and a monophyletic genus *Griffinia*. This lineage is suspected to be the oldest of the neotropical Amaryllidaceae (Meerow et al., 2000).

TRIBE GRIFFINEAE RAVENNA

Genus *GRIFFINIA KER GAWLER*

Plant perennial bulbous herb, terrestrial. *Bulb* tunicate, sub-globose, globose to ovoid. *Leaves* persistent or deciduous, distichous, petiolate; laminae ovate, elliptic to lanceolate. *Inflorescence* scapose, scape solid, 2-edged, terminating in an umbel (a series of reduced helicoid cymes), 2–24-flowered, enclosed in 2 partially fused spathe bracts. *Flowers* zygomorphic, pedicellate to nearly sessile, diurnal or nocturnal. *Perianth* epiperigynous or epigynous; tube present, variable in length; tepals linear to obovate, the outer whorl of tepals apiculate. *Stamens* 5 or 6, unequal in length. *Ovary* oblong, 3-carpellate; ovules 2–16 per locule; style filiform, declinate; stigma simple, capitate. *Fruit* a locucidal capsule, 3-valved, nodding. *Seeds* 1–3 per locule, lacking phytomelan, globose, turgid, with a whitish testa. *Chromosome number* $2n = 20, 30$.

TYPE: *Griffinia hyacinthina* (Ker Gawl.) Ker Gawl. *Edward's Bot. Reg.* 6 sub t. 444. 1820. *Amaryllis hyacinthina* Ker Gawl. *Edward's Bot. Reg.* 2: sub t. 163. 1816.

Key to the species of *Griffinia*

1a. Scape (4–) 5–20 (–24)-flowered; perigone blue, lilac and/or white, flowers diurnal, lacking scent; stamens five or six, five declinate, one assurgent or suppressed; ovules 2–8 (–10) per locule. .....Subgenus *GRIFFINIA*

2a. Leaves immaculate, petiole thick and rounded abaxially, inflorescence 10–15 (–24)-flowered; flowers cernuous; stamen number 5+1 consistently (5 declinate, in two ranks and one assurgent and appressed against the uppermost, outer tepal); lowermost tepal entire; ovules per locule 2 (-4); perigonal tube continuous (and concolorous) with the pericarp; insertion of floral parts epiperigynous.

3a. Lamina less than 18 cm long, ovate to oblong, petiole less than 13 cm long; perianth less than 3.5 cm long, lilac, whole-colored, perigonal tube less than 1 cm long.

4a. Lamina distinct from petiole; perianth less than 2.0 cm long. .....1. *G. parviflora*

4b. Lamina gradually tapered into petiole; perianth ca. 2.5–3.5 cm long. .....2. *G. intermedia*

3b. Lamina 20–25 cm long (or longer), 10–14 cm broad, petiole up to 24 cm long; perianth greater than 4 cm long, lilac and/or white; perigonal tube ca. 2–5 cm long.

5a. Leafbase cuneate (petiole winged distally); flowers pure white. .....3. *G. alba*

5b. Leafbase shortly attenuate (petiole not winged distally); flowers lilac with white in the basal portion of the perigone.

6a. Lamina ca. 12-nerved on each side of the midrib with sunken transverse striae diagonally intersecting the parallel veins; scape 20–24-flowered. .....4. *G. ornata*

6b. Lamina ca. 20-nerved on each side of the midrib with pronounced square-meshed, coarse, prominent reticulations; scape 8–13-flowered. .....5. *G. hyacinthina*

2b. Leaves sometimes maculate, petiole flattened: inflorescence 4–10 (–11)-flowered; flowers horizontal; lowermost tepal revolute; stamens typically 5, in two ranks (the sixth if present divaricate, not appressed to the upper, outer tepal); perigonal tube not continuous with the pericarp (pericarp green in color); insertion of floral parts epigynous.

7a. Leaves lanceolate to ovate, variously speckled whitish.

8a. Tepals with distinct white and lilac longitudinal zones of coloration.

9a. Leaf margins entire; tepals oblanceolate, bluish-lilac. .....6. *G. liboniana*

9b. Leaf margins undulate; tepals linear, violet-red. .....7. *G. aracensis*

8b. Tepals lilac apically, white proximally, not divided into two distinct longitudinal zones of coloration. .....8. *G. espiritensis*

7b. Leaves lanceolate, solid green.

10a. Leaves elliptic; scape 7–11-flowered; tepals violet-blue, ca. 30 mm long. .....9. *G. rochae*

10b. Leaves lanceolate; scape 4–6-flowered; tepals pale lilac, 14–16 mm long. .....10. *G. itambensis*

1b. Scape 2–3 (–4)-flowered, perigone white, flowers 15–18 cm long, nocturnal, fragrant; stamen six in three ranks of two, declinate, resting on the lowermost tepal, ovules 10–16 per locule. .....Subgenus *HYLINE*

11a. Perigonal tube ca. 1 cm Long; tepals linear, slightly recurved. .....11. *G. gardneriana*

11b. Perigonal tube ca. 5–6 cm Long; tepals oblanceolate, reflexed. .....12. *G. nocturna*

GRIFFINIA Subgenus *GRIFFINIA* RAVENNA *Plant Life*, 25: 62. 1969. TYPE: *Griffinia hyacinthina* (Ker Gawl.) Ker Gawl., *Edward's Bot. Reg.* 6 sub t. 444. 1820.

Leaves persistent; laminae may be variously maculated whitish or greyish. *Flowers* diurnal. *Perianth* epiperigynous or epigynous, lilac, lilac and/or white in color; tube present, reduced in the small-flowered taxa; tepals arranged in a 3+2+1 manner, three upper broader and ascending, two lateral and narrower, the lower narrowest descending, segments linear to obovate, acute. *Stamens* 5 declinate and 1 assurgent (often suppressed in the small-flowered taxa); pollen whitish. *Ovary* with 2–10 ovules per locule. *Chromosome number* $2n = 20, 30$.

1. ***Griffinia parviflora*** KER GAWLER. In *Edward's Bot. Reg.* 6: sub t. 511. 1821. (Fig.4). TYPE: A type specimen has not yet been located.

Bulb 4–5 (-7.5) cm in diam., subglobose; neck absent. Leaves ca. 18-29 cm long, lamina ovate, solid green in color, up to ca. 8 cm broad. Petiole and scape with reddish pigmentation near the bases. Scape slender, ca. 20–25 cm tall, (8-)10–15-flowered. Perianth epiperigynous, forming a true hypanthium continuous with the pericarp; tube, about 3 mm long; tepal segments oblong, obtuse, ca. 2 cm long, pale lilac. Stamen 6, arranged with five declinate and one assurgent. Chromosome number $2n = 20$.

Griffinia parviflora, described from the state of Bahia, lacks information regarding type locality. Plants occur in Southern Bahia south to Espirito Santo in the understory of the Mata Atlântica's thick primary and secondary growth rainforests.

2. ***Griffinia intermedia*** LINDLEY. in *Edwards Bot. Reg.* 7: sub t. 990. 1826. TYPE: A type specimen has not yet been located.

Bulb 5–8 cm diam., ovoid. Leaves solid green in color. Scape ca. 30 cm tall; 6–10-flowered; perianth epiperigynous, forming a true hypanthium continuous with the pericarp; tepals pale lilac, oblong, obtuse. Stamens 6, five declinate and one assurgent.

The original description of *G. intermedia* lacks detailed measurements and collection information. *Griffinia* intermedia was described from the state of Rio de Janeiro as intermediate between *G. parviflora* and *G. hyacinthina*. Floral morphology is well described and is similar to that of *G. parviflora* and *G. hyacinthina*. The scape is about 30 cm tall and 6–10-flowered. The flowers are most similar in shape to those of *G. parviflora*.

3. ***Griffinia alba*** PREUSS and MEEROW. (Novon: in press). TYPE: BRAZIL. TAPERA, PERNAMBUCO: collected from wooded habitat, 16 Nov 1936, *A. Pickel 2907* (HOLOTYPE: US!).

Leaves to 72 cm long; lamina ovate to elliptic, to 12–15 cm broad, solid green in color. Scape 35–38 cm tall; umbel 16–17-flowered. Perianth epiperigynous, forming a true hypanthium continuous with the pericarp; tube ca. 1.3–1.5 cm long; tepals entirely white, 4–5 cm long. Stamens 6, five declinate and one assurgent.

Griffinia alba is endemic to Northeastern Brazil and is known from a single locality in Tapera, Pernambuco. *Griffinia alba* closely resembles *G. hyacinthina*, but differs from that species by its longer pedicels, pure white flowers, tepal segments more linear, cuneate leaf base gradually tapering into the petiole, and geographical distribution. Based upon a preliminary morphological-based cladistic analysis, *G. alba* is sister to *G. hyacinthina*. *Griffinia alba* is the first pure white-flowered species described in the subgenus *Griffinia*.

4. ***Griffinia ornata*** MOORE in *Gard. Chron.* I: 266. 1876. TYPE: A type specimen has not yet been determined.

Bulb to ca. 10–11 cm in diam.; neck 5–10 cm long. Leaves elliptic, with distinctive venation: the parallel veins intersected diagonally by reticulate striae, solid green in color. Scape 30–45 cm tall, (18-) 20–24-flowered. Perianth epiperigynous; tepals lilac fading white in the center, tepal segments linear-lanceolate. Stamens 6, five declinate and one assurgent.

The original description of this species is rather vague. Detailed measurements, descriptions of the perigonal tube and collection and locality information are lacking. The author is unaware of any reported collections since 1875. It is uncertain whether or not this is a valid species or a form of *G. hyacinthina*. Like that species, *G. ornata* is from Rio de Janeiro and has large, thick, broad leaves, large lilac and white flowers with acute apices. The flowers are reportedly larger and greater in number (18–24) than *G. hyacinthina*. The leaf venation pattern in *G. ornata* is reportedly different of that observed in *G. hyacinthina* (*Moore, 1876*).

5. ***Griffinia hyacinthina*** (KER GAWLER) KER GAWLER. In *Edwards Bot. Reg.* 6. Sub t. 444. 1820. (Fig. 5). TYPE: A type specimen has not yet been located. *Amaryllis hyacinthina* Ker Gawl. in *Edward's Bot. Reg.* 2: sub t. 163. 1816. *Lycoris hacinthina* (Ker Gawl.) Herbert in *Curtis' Bot. Mag.* 47: sub t. 2113. 1819. *Amaryllis dryades* Vellozo in *Flor. Flum.* Liber primus. 130,

Icones, vol. iii. Sub t. 117. 1824. TYPE: not seen, undetermined. *Griffinia dryades* (Vell.) Vell. in *Flor. Flum.* Index, 3. 1827; Roemer in *Syn Ensat. Fase.* 4 (1) 32. 1847. *Griffinia hookeri* Kraenzl. in *Engl. Bot. Jahrb.* 1. Beibl. 112, 7. 1913.

Bulb to 7–8 cm in diam., subglobose; neck ca. 4–7 cm. Leaves 2–5, petiolate, ovate-elliptic, 18 to 45 cm long and 7 to 15 cm broad, solid green in color. Petiole and scape with reddish pigmentation near the bases. Scape stout, ca. 30–60 cm (taller than the leaves), 8–12 (-13)-flowered. Perianth epiperigynous, forming a true hypanthium continuous with the pericarp, to 10 cm long; tube variable in length, up to 2.5 cm.; tepals lilac with white in the center. Stamen 6, five declinate and one assurgent. Chromosome number $2n = 20$.

Martius (1871) considered *Griffinia dryades* Hooker to be a synonym of *G. hyacinthina*. Based on the available evidence of the type specimen (K) of *G. dryades*, the recognition of *G. dryades* as a synonym of *G. hyacinthina* is justifiable. The description of *G. dryades* indicates that flowers are slightly larger in size and are borne on longer pedicels. Like *Griffinia hyacinthina*, which was described from the state of Rio de Janeiro; both are also known to occur in the state of São Paulo. The degree of natural variation of *G. hyacinthina* is uncertain. Baker (1888) mentions a small-flowered variety, *G. hyacinthina* var. *micrantha*. *Griffinia ornata* is another species of similar stature, but with an increased number of flowers per scape, also known from Rio de Janeiro.

Griffinia liboniana complex

Within this informally recognized group, there are several species. The inter- and infraspecific relationships within this complex are uncertain. However, this subgroup of subg. *Griffinia* is a monophyletic group (Preuss, 1999), in which *Griffinia liboniana* is the oldest named taxon. The diagnosis for the *Griffinia liboniana* complex is as follows: leaves petiolate to subpetiolate, solid green or variously speckled white; petiole and scape lacking reddish pigmentation; insertion of floral parts epigynous; perigonal tube reduced, not continuous with the pericarp; the upper episepal stamen typically lacking, when present not adpressed to the dorsal segment.

6. ***Griffinia liboniana*** MORREN. In *Ann. Soc. Roy. Agr. Bot.* 1: 143. 1845. (Fig. 6 and 7). TYPE: not seen, undetermined. *Liboniana bicolor* Lemaire in Jard. Fleur. vol. iii: sub t. 290. 1853.

Bulb 3–5 cm in diam., neck ca. 2 cm long. Leaves elliptic to broadly ovate, profusely speckled whitish or solid green. Petiole and scape lacking reddish pigmentation. Scape to ca. 20–38 cm tall, 4–9-flowered. Perianth epigynous; tepals lilac apically fading to white in the center and base, two lateral with two longitudinal zones of coloration: lilac on one side, white on the other side, white basally, oblanceolate, slightly unguiculate. Stamens 5 or 6, five declinate, the sixth assurgent or supressed. Chromosome number $2n = 20, 30$.

Griffinia liboniana Morren (1845) was collected from the landlocked state of Minas Gerias and described with an accompanying illustration, possibly the holotype. Lemaire (1853) published another "more accurate" interpretation. However, the two interpretations of the same plant vary considerably. The two plates vary considerably in the floral form and color. This could be due to the artists' interpretations, natural variation, or, alternatively, a different "entity" was represented by each of the two plates. Both plates represent a subpetiolate, spotted-leaf *Griffinia* and are considered to represent, in part, the natural variation found in *G. liboniana*. This brings to point the issue of just what the name *Griffinia liboniana* represents. A type specimen for *G. liboniana* has not yet been located. Ravenna (1974) reported the "Rediscovery of *Griffinia liboniana*" from plants collected by A. P. Duarte, which were deposited into the personal herbarium of P. Ravenna (Herbarium Ravennae). Until further collections from Minas Gerais can be examined and compared to those from Bahia, this issue is unable to be resolved.

7. ***Griffinia aracensis*** RAVENNA. In *Plant Life*, 30: 69. 1974; and in *Plant Life* 34: 82. 1978. (Fig. 8). TYPE: BRAZIL: Minas Gerias, Serra dos Aracás, near Matozinhos, 26 Oct 1959 E. P. Heringer 72–40 (HOLOTYPE: UB!).

Bulb ca. 2 cm diam.; neck 6–10 mm. Leaves variable in length, from 7–25 cm long and to ca. 5 cm broad, lanceolate, lamina solid green or variously maculated whitish, margins undulate. Scape 7–12 (-15) cm. tall; 4–7-flowered. Perianth epigynous; tepals lilac in the upper portion and white in the lower portion, the two lateral tepals with two longitudinal zones of coloration: lilac on one side, white on the other side, tepal segments (narrowly) oblanceolate. Stamens 5 or 6, five declinate, the sixth assurgent or supressed. Chromosome number $2n = 20$.

Griffinia aracensis was described from a single collection from Serra dos Aracás, near Matozinhos, Minas Gerais. Since that collection, there have been no other reports of collections from Minas Gerais for this species. However, the range of this species extends eastward into Bahia (Preuss, 1999). This species is most easily identified by its narrow tepals and undulate leaves.

Fig. 1. Fruit of *Griffinia espiritensis*.

Fig. 2. Seed of *Griffinia espiritensis*.

Fig. 4. *Griffinia parviflora* (Ker Gawler) Ker Gawler

Fig. 5. *Griffinia hyacinthina* Ker Gawl. Photo by A. F. C. Tombolato.

Fig. 6. *Griffinia liboniana* Morren.

Fig. 7. *Griffinia liboniana*, inflorescence.

Photos by Kevin Preuss unless otherwise stated.

Fig. 8. *Griffinia aracensis* Rav., non-spotted leaf form.

Fig. 9. *Griffinia espiritensis* Rav., a $2n = 30$ form.

Fig. 10. *Griffinia espiritensis* a $2n = 20$ form.

Fig. 11. *Griffinia rochae* Morel. Photo by A. W. Meerow.

Fig. 12. *Griffinia gardneriana* (Herb.) Rav. Photo by J. Dutilh

Fig. 13. *Griffinia nocturna* Rav. Photo by J. Dutilh.

8. *Griffinia espiritensis* RAVENNA. In *Plant Life*, 25: 67. 1969. (Fig. 9, 10). TYPE: BRAZIL, Espírito Santo, Sooretama Biological Reserve, on the way to the waterfall, Dec 1965, *P. Ravenna 399* (HOLOTYPE: HERB. RAVENNAE).

Bulb 2–5 cm in diam.; neck to ca. 2 cm long. Leaves elliptic-lanceolate (-ovate), 4–8 cm broad, solid green or variously maculated whitish. Scape 9–38 cm tall; umbel 5–10 flowered. Perianth epigynous, to 3.3 cm long; tube ca. 2–3 mm long, tepals various shades of lilac with white in the center, tepal segments oblanceolate. Stamens 5 or 6, five declinate, the sixth assurgent or supressed. Chromosome number $2n = 20, 30$.

This species group is a monophyletic subgroup within the *G. liboniana* complex (Preuss, 1999). *Griffinia espiritensis* was described from the state of Espírito Santo (Ravenna, 1969). The range of this species extends northward to Bahia (Preuss, 1999). *Griffinia espiritensis* is polymorphic and a highly variable species (Fig. 9). Leaves vary in form from narrowly lanceolate to ovate, and may be solid green in color in some forms or variously spotted in other forms. The flowers greatly vary in size and shape, and ranges in color from pale lilac to deep purple with white in the center.

9. *Griffinia rochae* MOREL. In *Baileya*, vol. 8: 133. 1960; *Baileya*, vol. 9: 28. 1961. (Fig. 11). TYPE: BRAZIL. Prov. Rio: Xerem, Cult. In greenhouse, Centre National de Recherches Agronomiques, Versailles, 15, Feb 1960, *G.M. Morel, s.n.* (HOLOTYPE : BH).

Bulb globose, ca. 3 cm in diam.; neck ca. 1 cm. Leaves 10–16 cm long; lamina oblong, solid green. Scape ca. 20 cm tall; umbel 6–8-flowered. Perianth epigynous; tube ca. 1–2 mm long; tepals bluish-lilac with white in the center. Stamens 5 or 6, five declinate, the sixth assurgent or supressed. Chromosome number $2n = 20$.

Griffinia rochae is endemic to Rio de Janeiro and represents the southernmost limit of distribution for the small, blue-flowered taxa. This species is allopatric in respect to the other small, blue-flowered taxa. *Griffinia rochae* is the smallest species (in stature) of the genus. The character of leaf-spotting has not been reported or observed in this taxon. The chromosome number of $2n = 22$ (Morel 1960) is dubious; upon closer examination, the number $2n = 20$ was observed (Preuss, 1999).

10. *Griffinia itambensis* RAVENNA. In *Plant Life*, 30: 70. 1974. TYPE: BRAZIL: Minas Gerais, mun. Itambe, about 5 km directly west and north of Santo Antonio do Itambe, south-eastern drainage of Pico de Itambe, Nov. 9, 1972, *W. R. Anderson et al.* (HOLOTYPE: HERB. RAV; ISOTYPE: NY!).

Bulb subglobose, ca. 2.5– cm in diam.; neck almost obsolete. Leaves lanceolate, 12–25 cm long, 1.5–2.2 cm broad, solid green. Scape to ca. 19 cm tall; umbel 7–11-flowered, Perianth epigynous; tube ca. 15 mm long; tepal segments oblanceolate, lilac and white in the lower portion, ca. 14–16 mm long. Stamens 5 or 6, five declinate, the sixth assurgent or supressed

Griffinia itambensis Rav. has been recognized by its small flowers (the smallest of the genus) and narrow, lanceolate leaves, which lack speckling. *G. itambensis* is possibly a variety of *G. espiritensis*. In a phylogentic analysis based on morphology, *G. itambensis* is part of the monophyletic *G. espiritensis* group (Preuss, 1999). Unfortunately, an attempt to extract DNA from the type specimen for a phylogenetic study of the ITS region was unsuccessful. This entity is represented by a single collection from a population located near the municipal of Itambé, Minas Gerais. The population occurred at an altitude of about 950 m on a hillside with secondary growth forest and bracken covered "campo" with blocky sandstone and sandy soil sloping down to a river (Ravenna, 1974a).

GRIFFINIA Subgenus HYLINE (HERBERT) RAVENNA *Plant Life*, 25: 62–63. 1969. *Hyline* Herbert, *Curtis's Bot. Mag.* 66: sub t. 3779. 1841. TYPE: *Griffinia gardneriana* (Herb.) Rav., *Curtis's Bot. Mag.* 66: sub t. 3779. 1841.

Bulb, ovate (-subglobose). *Leaves* deciduous; lamina oblanceolate to lorate, slightly falcate. *Scape* 2–3-flowered. *Flowers* nocturnal, ephemeral, scented. *Perianth* white in color, epiperigynous, forming a true hypanthium continuous with the pericarp, tube variable in length, tepal segments linear to oblanceolate. *Stamens* 6, in 3 ranks; fasciculate; filaments with style declinate; pollen yellow. *Ovary* with 12–16 ovules per locule. *Seeds* 2–3 per fruit. *Chromosome number* $2n = 20$.

11. ***Griffinia gardneriana*** (HERBERT) RAVENNA in *Plant Life*, 25: 62–63. 1969. (Fig. 12). TYPE: BRAZIL, Ceará, dry woods, Oct 1838, *Gardner 1854* (HOLOTYPE: K!). *Hyline gardneriana* Herbert in *Curtis's Bot. Mag.* 66: sub t. 3779. 1841. *Hyline Worsleyi* Mallet in *Gard. Chron.* III: 26. 102. 1899.

Bulb ca. 4–7.5 cm in diam., subglobose; neck ca. 1.5 cm long. Leaves lorate to lanceolate, nearly 50 cm long and ca. 6 cm broad. Scape 17–35 cm tall, 2 (-3)-flowered; pedicels ca. 2–3 cm long. Perianth epiperigynous; tube short ca. 2 mm, continuous with the pericarp; tepals ca. 15– 17 cm long, oblanceolate, the 5 upper ones strongly recurved, the lowermost straight and supporting the filaments. Chromosome number $2n = 20$.

Griffinia gardneriana has rarely been collected. This species is endemic to the dry woods of the cerrado and caatingas of Ceará, Pernambuco and Maranhão. Its range does not overlap with that of its sister species (*G. nocturna*). *Griffinia garderiana* represents the northernmost limit of distribution for both the genus and subgenus. The bulbs were once used by the indigenous peoples as an hemetico-purgative (Herbert, 1841).

12. ***Griffinia nocturna*** RAVENNA in *Plant Life*, 25: 62–63. 1969. (Fig. 13). TYPE: BRAZIL, Goiás, deciduous or semideciduous woods near the of Goiás, April 1966, *Ravenna 531* (HOLOTYPE: HERB. RAVENNAE). *Griffinia rostrata* Ravenna in *Plant Life*, 34: 82. 1978. (HOLOTYPE: UB; ISOTYPE: K!).

Bulb to 7 cm in diam, ovoid-globose; neck ca. 1 cm. Leaves oblanceolate, ca. 40–50 cm long,. Scape 14–35 cm tall; 3–4-flowered; flowers nearly sessile, pedicels ca. 3 mm long; scented. Perianth epiperigynous; tube ca. 5 cm long, continuous with the pericarp; tepals linear, ca. 11–15 cm long, slightly recurved, the lowermost straight and supporting the filaments. Stamens 6, fasciculate, declinate; pollen yellow. Chromosome number $2n = 20$.

Griffinia nocturna has a vast distribution in arid and semi-arid regions ranging from Mato Grosso do Sul, Goiás, Tocantins and Pará, and possibly Bahia. *Griffinia rostrata* Ravenna was described from a single collection of a plant in fruit (flowers were lacking) with three capsules. The locality was near Xavantinas, Mato Grosso do Sul, a state that had not previously yielded any other collections of *Griffinia*, but of typical ecology for *G. nocturna*., which is well-represented in the state of Goiás, immediately to the north. The seeds were described as "subpyriform, fleshy, reddish in the herbarium, bearing a thick unilateral aril" (Ravenna, 1978a). The description of the seed as arilate needs further corroboration as is was not evident from the material I examined. This is the only report of fruit and seed for the subgenus *Hyline*. Vegetatively, *G. rostrata* appears identical to *Griffinia nocturna*, and there is no evidence to warrant treating it as a distinct species. This collection represents the southernmost limit of distribution of the subgenus *Hyline*.

Species Dubium

Griffinia concinna (MARTIUS) RAVENNA in *Plant Life*, 27: 84. 1971. *Crinum concinnum* Mart. *In* Roemer et Schultes, *Syst. Veg.*, 7: 857. 1830.

Originally described as *Crinum concinnum* Martius, the placement of this taxon under the genus *Griffinia* is questionable. This plant was described

from a solitary scape in flower (Ravenna, 1971). The bulb and leaves, which would indicate if this plant was a *Crinum*, are lacking on the herbarium specimen, but a photo of the type suggest to me a species of *Crinum* subg. *Codonocrinum*, probably introduced from Africa. Unfortunately, according to Ravenna (1971), the type locality has been much modified by man, and, apparently, these plants have disappeared from that place.

ECOLOGICAL PRESSURES

Most species of *Griffinia* grow in the lush, wet understory of tropical forests of eastern Brazil. The Brazilian Atlantic Forest has undergone tremendous modification (Dean, 1995). The once contiguous forests of the Mata Atlântica, which extended inland from the coast about 100 kilometers in the north and more than 500 kilometers in the south, encompassed about a million square kilometers and ranged from 8° to 28° South latitude (Dean, 1995). A survey of the entire Atlantic Forest showed that by 1990 only a little more than eight percent, or 83,500 square kilometers, remained (Farez, 1993). Contiguous chunks of forest are now rare.

Upon visiting several previous collection sites of *Griffinia*, it was evident that most sites were no longer able to sustain once extant populations due to extreme modification of the terrain. Like many other genera of tropical plants, animals, and insects, *Griffinia* is experiencing ecological pressure from the severe devastation, modification, and loss of its native tropical forests. Fortunately, members of the genus can be found in cultivation in Brazil, where they are referred to as *carícia*. One can only hope that this endangered, elegant, and charming genus will be protected, and that conservation efforts will prevail.

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Breeding Amaryllis

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Hippeastrum Herbert, the amaryllis, has yielded popular large-flowered hybrids over a 200 year breeding history. Bulbs are produced for indoor forcing and, to a lesser extent, garden use in mild winter areas (USDA Hardiness Zones 7B–11). The amaryllis is much appreciated by gardeners for its ease of culture, while amateur plant breeders have found it an easy and rewarding group to hybridize.

Hippeastrum consists of 50–60 entirely New World species, though one species, *H. reginae* Herbert, appears to have been introduced to Africa. The species are concentrated in two main areas of diversity, one in eastern Brazil, and the other in the central southern Andes of Peru, Bolivia and Argentina, on the eastern slopes and adjacent foothills. A few species extend north to Mexico and the West Indies. The genus is essentially tropical and subtropical, though some species occur far enough south of the equator and at sufficient elevation to be considered temperate plants. Little of this genetic diversity is represented in modern, commercial amaryllis hybrids. Early hybrids were produced from a relatively small number of species, mainly *H. vittatum* Herbert, *H. reginae*, *H. puniceum* (Lamarck) Voss, *H. aulicum* Herbert, *H. psittacinum* (Ker Gawler) Herbert, *H. striatum* (Lamarck) H. E. Moore, and *H. reticulatum* Herbert (Bell, 1973a; Cage, 1978a; Shields, 1979; Traub, 1934a, 1958).

The taxonomic relationships among *Hippeastrum* species have yet to be carefully elucidated. Various botanical groupings have been proposed (Traub and Moldenke, 1948) but are of little significance to the plant breeder since virtually all diploid *Hippeastrum* species, regardless of their geographic origins, have been successively interbred. Species or species groups of special interest are discussed later in this chapter. It should be noted that a number of species sometimes offered as "dwarf amaryllis" in specialist's catalogs (and, in some cases, originally described as species of *Hippeastrum*) are now properly recognized as belonging to the genus *Rhodophiala* Presl.. No true *Hippeastrum* has been successfully bred with a *Rhodophiala* species. Likewise, the Brazilian blue amaryllis, *Worsleya rayneri* (Hook. f.) Traub and

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Moldenke (synonym: *Hippeastrum procerum*), has never been successfully hybridized with *Hippeastrum*. From time-to-time, there have also been reports of wide intergeneric crosses between *Hippeastrum* and other genera of Amaryllidaceae such as *Crinum* or *Eucharis*. There is no evidence that these hybrids are genuine. To date, the only reported intergeneric hybrids involving *Hippeastrum* that appear to be true are those involving *Sprekelia formosissima* (L.) Herbert (Aztec lily), though it should be noted that two species of amaryllis, *H. angustifolium* Pax and *H. cybister* (Herbert) Bentham and Hooker, have flowers which resemble those of *Sprekelia*.

HISTORY OF AMARYLLIS BREEDING

A detailed history of amaryllis breeding and cultivation can be found in Traub (1958) and Read (this issue) and will only be summarized here. *Hippeastrum* x 'Johnsonii,' generally acknowledged as the first amaryllis hybrid, was a primary hybrid of *H. vittatum* and *H. reginae* made in England in 1799 (Traub, 1934a). Many additional hybrids were reported during the first 25 years of the 19th century as new species were collected in South America and imported to Europe. The two most significant developments in amaryllis breeding were the development of the Reginae and Leopoldii strains of hybrids.

The Reginae strain were developed by Jan de Graaff of Holland and his two sons in the middle of the 19th century by breeding *H. vittatum* and *H. striatum* with *H. psittacinum* and some of the better hybrids available in Europe. The clones 'Graveana' and 'Empress of India' were particularly outstanding and figured importantly in successive breeding efforts.

The introduction of *H. leopoldii* Dombrain and *H. pardinum* (Hook. f.) Lemaire from the Andes by the plant explorer Richard Pearce in the employ of the British firm Veitch and Sons would have lasting impact on the future of amaryllis hybridization. Both species are notable for their large, wide-open, and relatively symmetrical flowers. When bred with the best of the Reginae strain of hybrids, a race of large- and very open-flowered progeny were developed, the best of which carried 4–6 flowers on the scape. Veitch and Sons dominated the development of the Leopoldii strain and thus European amaryllis breeding well into the first quarter of the 20th century. The best of these Veitch hybrids set the standards that have largely since dominated commercial amaryllis development.

Two additional hybrid strains were developed but either over-shadowed by the Reginae and Leopoldii types or else never widely distributed. The

Vittatum strain was produced by breeding *H. vittatum* with other species and hybrids. The majority originated in France, but England was a secondary producer as well. The late-summer to fall blooming Reticulatum hybrids (based on the Brazilian species *H. reticulatum*; see discussion below) were generally smaller statured than other hybrids, evergreen, and featured a white or yellowish stripe down the midrib of the leaf (transmitted by *H. reticulatum* var. *striatifolium*).

The late 19th century to the early 20th saw a modicum of amaryllis breeding efforts in the United States, primarily in Texas, California and Florida. Luther Burbank developed a large-flowered strain based on the European Reginae and Leopoldii groups. However, the greatest American contributions to amaryllis hybridization were those of two Florida breeders, Henry Nehrling and Theodore Mead (Bell, 1973a; Hayward, 1934; Traub, 1934b). The Mead hybrids in particular, originating from Nehrling's germplasm, have contributed to some modern hybrids when crossed with Ludwig or other Dutch stock (Bell, 1973a). Though the Mead hybrids did not match the European strains in flower size and number of scapes produced, they were reliable and vigorous performers under Florida garden conditions (Bell, 1973a; Hayward, 1934, Traub, 1958). As amaryllis production in Florida faded, the result of disease, competition, and failures in quality control, much of this germplasm has been lost.

After the first two decades of the 19th century, amaryllis breeding and production in Europe declined, as much the result of two world wars as for any other reason. The exception was the Netherlands, and today, the center of modern amaryllis production and breeding is Holland. The large-flowered Ludwig strains (for example, 'Apple Blossom', Dazzler', 'Dutch Belle', White Christmas') have rapidly become the dominant genotypes among Dutch amaryllis (Ludwig and Co., 1948). Another important Dutch cultivar group is the Gracilis strain of dwarf, multiflora types (*H.* 'Firefly' and 'Scarlet Baby', for example). The strain was originated by H. Boegschoten by breeding *H. striatum* with large-flowered hybrids and developed commercially by the van Meeuwan and Sons Company. South Africa has also now become an important breeding center and exporter of amaryllis (Barnhoorn, 1976, 1991; Buck, 1961; Goedert, 1961) as well, particularly the Hadeco strain (Barnhoorn, 1976, 1991).

Before ending this short history, the legion of amateur breeders of amaryllis, too numerous to list by name, in America, Europe, Asia and Australia should be acknowledged. From time-to-time, selections from these

small-scale breeding programs have been offered commercially or purchased as breeding stock by large commercial endeavors.

IMPORTANT TRAITS AND BREEDING OBJECTIVES

The emphasis in commercial breeding efforts in amaryllis, with exception of the Gracilis strain, has traditionally been on large flower size, traits attributable specifically to genes originating in *H. leopoldii* and *H. pardinum* (Bell, 1973a; Shields, 1979; Traub, 1958). Commercial breeding efforts subsequent to the initial flurry of primary hybridization has largely been concentrated among the hybrids themselves, leading to a greater complexity of parentage (much without documentation) and dilution of many of the unique characteristics of the original component species (Bell, 1973a, b; Cage, 1978a; Shields, 1979).

The result of these constraints, whether voluntary or involuntary, on commercial amaryllis breeding has been a similarity to many of the modern hybrids. The flowers, while large, tend to be of the wide, flat, "dinner-plate" type with little variety of form and limited variation in color (Doran, 1982), despite repeated call for renewed programs of interspecific hybridization (Bell, 1973a, 1977a; Buck, 1978; Cage, 19878a; Doran, 1982; Shields, 1979).

The pursuit of novelty in amaryllis hybrids has largely been the province of amateur breeders and collectors, most of whom have little inclination to commercially exploit their hobby or have failed in their attempts to do so (Cage, 1978b, Cothran, 1979; Doran, 1982; Wilson, 1981). Breeding efforts by amateurs have largely been ignored by European breeders with the possible exception of attempts to develop a large-flowered yellow hybrid (Blossfeld, 1973; Cothran, 1979, 1980, 1981, 1984, 1985; Goedert, 1982). There has also been some commercial interest in double-flowered varieties (Bell, 1977b).

Amaryllis hybrids could be improved in a number of ways (Bell, 1973a, 1977a; Cage, 1978a; Shields, 1979). These include novel attributes of flower form (e.g.: trumpet or long-tubed perianth, novel pigmentation patterns), re-introduction of fragrance, evergreen foliage, repeat bloom, as well as along more strictly cultural criteria [resistance to hippeastrum mosaic virus and red scorch (*Stagonsopora curtisii*)].

BREEDING AND PLOIDY LEVEL

The overwhelming majority of *Hippeastrum* species are diploid, with somatic chromosome number of $2n = 22$ (Arroyo, 1982; Flory and Coulthard, 1981; Naranjo and Andrada). Virtually all of the complex hybrid

material presently in cultivation is tetraploid (Bell, 1973a, b, 1977a; Shields, 1979), a result of both selection for tetraploid progeny (often associated with plant and flower size increases in hybrid amaryllis) and incorporation of a few natural tetraploid species in early hybridization efforts (some forms of *H. striatum*, for example). A few species of *Hippeastrum* have been reported with higher ploidy levels then 4*n* (Traub, 1958), but I am not aware of any breeding efforts with them.

The concentration of recent commercial breeding efforts among the various populations of tetraploids may exist for several reasons: 1) desirable characteristics of flower size, scape number, and plant vigor are already stabilized in the hybrid races; 2) sterile triploid progeny result when diploid species are crossed with tetraploid hybrids (Bell, 1973b, 1977a); 3) many of the diploid species are not readily available; and 4) self-incompatibility, which occurs in most diploid species and diploid hybrids, generally breaks down in the tetraploid hybrids (Bell, 1973a, 1977a; Cage, 1978a; Shields, 1979; Williams, 1980), thereby allowing breeders to obtain a segregating F_2 generation.

Breeding at the diploid level. The advantages of breeding among the diploid species of *Hippeastrum* (which constitute the majority) are 1) novel traits can only be found among the species, 2) diploid species are readily inter-fertile, 3) diploid F_1 hybrids can often be flowered in eighteen months or less from seed, and 4) hybrid vigor is frequently expressed in the F_1 generation in the form of higher scape and bud counts to the scape. The disadvantages are twofold. Firstly, self-incompatibility, which characterizes most wild species, carries over into the hybrids. I have even found that compatibility barriers between siblings of the same cross are more often the rule than the exception. Secondly, the green throat and/or floral tube of most species appears in the hybrids as well. By-and-large, this is considered an objectionable characteristic in the marketplace. Diploid hybrids will also have smaller flowers than the commercial Leopoldii-type cultivars.

Breeding diploids and tetraploids. It is generally conceived that diploid and tetraploid amaryllis are difficult to breed. Previous reports have stated that if diploids are used as maternal parents with tetraploid pollen, only sterile triploid progeny will result, while reciprocal crosses (tetraploid as seed parent, diploid as pollen parent) will rarely set any seed at all (Bell, 1973b, 1977a). The ovary may begin to swell with developing seeds but then aborts at a further point in time before full term. In the latter situation, progeny can sometimes be obtained through embryo rescue, in which the

developing ovule is excised from the ovary several days after pollination and grown on a sterile medium. This is probably beyond the resources of most amateur amaryllis hybridizers. However, in my experience, using tetraploid pollen on diploid seed parents can yield a small number of tetraploid progeny. Interestingly, when I have pollinated some diploid hybrids or species with pollen of many Dutch hybrids, a full and apparently normal seed capsule will develop. Most of the seeds, however, contain no embryo. Approximately 10% of the seed will germinate, and yield a mix of triploids and tetraploids. Unreduced gametes (that is, egg cells with 22 rather than the usual 11 chromosomes) in the diploid parent are the probable source of the few tetraploid progeny that occur in these crosses.

Triploids. The triploid progeny that usually result from $2n$ (diploid) x $4n$ (tetraploid) crosses of amaryllis are usually both self- and inter-sterile (Bell, 1973b). Rarely can they be bred with diploid species or hybrids, though techniques of embryo culture can be used to "rescue" progeny of such crosses, as long as fertilization has taken place and the developing seeds are placed in culture before the ovary begins to abort. Greater success has been reported crossing triploid amaryllis with tetraploids, perhaps due to some degree of random assortment of the third set of chromosomes during gamete formation (Bell, 1973b). Triploid intermediates of diploid species or hybrids may allow introgression of desirable species traits into established tetraploid cultivars without the rapid dilution of those traits that occurs with diploid-tetraploid crosses followed by exclusively tetraploid breeding.

Breeding tetraploids. The self-incompatibility of most diploid amaryllis almost invariably disappears in tetraploid hybrids and most tetraploid species (Bell, 1973a, 1977a; Cage, 1978a; Shields, 1979; Williams, 1980). Most tetraploids can be readily self-pollinated and inter-crossed with a resulting high percentage of viable seed. This has largely been the source of today's commercial amaryllis cultivars, and is the easiest breeding program for the interested amateur hybridizer to undertake, as much due to the wide availability of tetraploid hybrids as to the absence of compatibility barriers.

LESSER KNOWN USEFUL SPECIES AND SPECIES GROUPS FOR AMARYLLIS BREEDING PROGRAMS

Hippeastrum papilio (Rav.) Van Scheepen. First described in 1970, *H. papilio* may be the most significant amaryllis introduction in this century. The species is evergreen, and the foliage is quite handsome relative to most other *Hippeastrum*. The species flowers regularly in late winter or early spring,

though some growers have reported fall flowering as well. The species seems to be resistant (though not immune) to both hippeastrum mosaic virus and red scorch. The flowers, which last for at least a week on the plant, are laterally compressed, with broad lateral tepals that are attractively patterned with red to purple on a background of white and light green. The species is self-compatible (Bell, 1977a. *H. papilio* transmits foliage quality and evergreen nature to its F_1 hybrids. To retain the evergreen characteristic, however, subsequent progeny must have at least 50% *papilio* genes. The green background of the flower tends to muddy the colors of F_1 hybrids, but subsequent breeding with pure whites or clean pastel shades will bring out the rich magenta undertones of *papilio*. Due to *papilio*'s green background, it is probably not desirable to backcross *papilio*-hybrids to the species. F_1 hybrids of *papilio* are particularly vigorous and may regularly produce four, even five, scapes from older bulbs each season.

Trumpet-flowered white species. This group of *Hippeastrum* species have largely been ignored by breeders of commercial amaryllis hybrids in this century. The species are not well understood taxonomically. A number of erstwhile species have been included as variants of *H. argentinum* (Pax) Hunziker in some taxonomic accounts. For the purposes of this discussion, the original species designations will be followed. The two most useful species are *H. brasilianum* (Traub and Doran) Dutilh and *Hippeastrum fragrantissimum* (Cárdenas) Meerow. Both species have very large, every fragrant, long-tubed white flowers produced 2–4 on the scape that resemble Easter lilies (*Lilium longiflorum*). The flowers have heavy substance and are longer-lasting than some of the other species in this group. *H. brasilianum*, from the state of Espiritu Santo in Brazil, is most useful for breeders in warm climates. *H. fragrantissimum*, from Bolivia, requires cool temperatures during its long dormant period, and will transmit this requirement to its F_1 progeny. If subjected to long, hot, humid summers, the bulbs will decline. Other species include *H. solandriflorum* (Lindley) Herbert, a species broadly distributed through South America.

Hippeastrum reticulatum var. *striatifolium* Herbert. This variety of the Brazilian species *H. reticulatum* is notable for the distinct white midrib on the leaves. The flowers vary in color from pink to almost lavender, and in form from trumpet-shaped and nodding to more widely spreading. Unlike virtually all other species, the flowers appear in late summer to early fall, suggesting that there may be a photoperiodic response involved in scape emergence. At least some clones can be maintained with leaves year-round.

It is another one of the few species that can be successfully self-pollinated. The white striping of the leaves segregates in a 3:1 ratio among selfed progeny and the striping carries over into F_1 hybrids with other species (Bell, 1977a), suggesting a single gene with a dominant allele controls the character. Mixed population are usually observed in the wild in Brazil. Further breeding will, however, dilute the leaf striping unless hybrids are backcrossed to the species or to the F_1's. All clones (striped or not) of *H. reticulatum* are fairly compact plants and can also be useful for breeding smaller-statured hybrids. The species occurs in the understory of tropical forest and requires heavier shade than most other amaryllis species. This lower light requirement seems to be imparted to F_1 hybrids as well.

Breeding for yellow amaryllis. Despite the release in recent years of cultivars such as 'Yellow Pioneer', 'Lemon Lime' and 'Germa', a Leopoldii-type clear yellow amaryllis has remained elusive. Three species produce yellow flowers, *H. evansiae* (Traub and Nelson) H. E. Moore (Bolivia), *H. parodii* Hunziker and Coccuci (Argentina) and *H. algaiae* (Castellanos) Hunziker and Coccuci (Argentina), and, not surprisingly, breeding efforts for yellow have concentrated on these three. Of the three, *H. evansiae* is best adapted for growing in hot, humid climates. These species should be crossed only with green or white flowered species and hybrids, as brightly pigmented parents will mask expression of the yellow coloration in the progeny. Cothran (1979, 1980, 1981, 1984) has detailed his efforts (and trials) toward a large, yellow hybrid amaryllis.

Spider- or orchid- flowered species. Two species of *Hippeastrum* have unusual, highly asymmetrical flowers with narrow tepals that resemble the flower of Aztec lily (*Sprekelia formosissima*). The lower tepals form a tube around the staminal filaments and the style. *H. cybister*, from Bolivia, has green and maroon flowers, while *H. angustifolia*, from Brazil and Argentina, is red-flowered. The later species grows as an emergent aquatic plant along streambanks and in marshes, and has been observed with as many as nine flowers on the scape. Both impart some of their unusual character to their hybrids, especially F_1's with other diploid species. If bred to tetraploids, this unique characteristic is quickly diluted.

Species with high flower number. A number of *Hippeastrum* species regularly produce scapes with six to as many as nine flowers. This character is readily transmitted to their hybrids, sometimes through a second generation of breeding (Bell, 1977a). It appears to be a dominant character but is not inherited in simple Mendelian ratios, which may indicate that it is con-

trolled by more than one gene. It should also be noted that an increase in flower number sometimes accompanies increase in ploidy level. Species frequently holding more than four flowers on a scape include *H. cybister*, *H. angustifolium*, *H. breviflorum* Herbert, *H. reticulatum*, and *H. fosteri* (Traub) H. E. Moore.

Smaller-statured species. The success of the Gracilis strain of amaryllis indicate that there is interest in amaryllis hybrids with smaller flowers and more compact foliage. *H. striatum* has been the primary contributor to the Gracilis strain and is still an excellent choice for breeding with Dutch-type tetraploid hybrids with which it is readily compatible due to its own tetraploid genotype. The closely related *H. petiolatum* Pax ex Engl., also tetraploid, will produce Gracilis-like progeny when bred with large-flowered, tetraploid cultivars. Other dwarf species include *H. reticulatum*, discussed above, and *H. espiritense* (Traub) H. E. Moore.

BREEDING FOR SPECIFIC TRAITS

Color and pigmentation patterns. Little is known of the genetics of color inheritance in *Hippeastrum*. Anthocyanin pigments (reds) appear dominant over carotenoid-based pigments such as yellow. Green and white flowers are essentially without pigment expression. In green amaryllis flowers, chloroplasts present in the surface cells of the tepals are responsible for the color expression. They are presumably absent in white-flowered species or cultivars. If the goal is to preserve unique patterns of color in a species or hybrid, further breeding efforts should concentrate on parents with white or light pastel floral shades. Dark reds or pinks will usually "overwhelm" zonations of color on a white or greenish-white background, and the progeny will be mostly or entirely the color of the dark-colored parent (assuming that at least one parent is homozygous for red). If both parents have interesting patterns of pigmentation on a white or greenish-white background, the progeny frequently show novel combinations of these patterns. The amount of variation that will appear in an F_1 generation is directly proportional to the degree of heterozygosity in the parents for genes controlling color formation and expression. By repeatedly intercrossing progeny with the same flower color, generation after generation, it is possible to develop groups of seed propagated, true-breeding stock for flower color. This is, in fact, what a number of the early European and American breeders and producers did before the advent of large-scale vegetative propagation. Repeated selfing of self-compatible cultivars of pure color will also achieve these

results, but may also result in loss of vigor due to inbreeding depression. The concept of line-breeding, in which such inbred lines, highly homozygous, are then crossed to restore vigor, has never been applied to amaryllis.

Fragrance. From the behavior or hybrid progeny of crosses in which one parent is fragrant, it seems that fragrance in amaryllis is a recessive trait, though no genetic analysis of the characteristic has been performed. Progeny of two fragrant parents are usually fragrant. When a fragrant diploid is crossed to a non-fragrant diploid, the F_1 hybrids will often assort for this character, suggesting that the non-fragrant parent may be heterozygous for the fragrance gene (if indeed, a single gene is responsible). When non-fragrant diploids are crossed with fragrant tetraploids, the majority of the progeny are fragrant, perhaps due to the presence of two copies of the fragrance gene(s) in the F_1 genome. As is evident from the over-whelming lack of fragrance in many of the modern commercial cultivars, the trait is rapidly diluted and lost unless persistent backcrossing to the fragrant parent or further complex hybridization is performed using other fragrant species or hybrids. Fragrance also appears to be linked (at least phenotypically) with white or pastel-colored flowers in amaryllis.

Double flowers. Double flowered amaryllis are an acquired taste, but there is has always been some interest in them. The first reported double amaryllis was found in the wild in Cuba, a form of *H. puniceum* (Traub, 1958). Significant breeding for doubleness was first reported by McCann (1937, 1950). Additional tepal-like structures apparently result from transformations of both stamens and style (male and female reproductive structures). McCann's and other observations (Latapie and Latapie, 1982) on inheritance of the character indicate dominance for doubleness in breeding. Recent bulb catalogs have been offering some double-flowered cultivars ('Lady Jane', 'Pasadena', and 'Double Picotee'). Double-flowered amaryllis may not have any functional reproductive parts or may produce some pollen-containing anthers at the ends of some of the transformed, petal-like stamens. This pollen can used for successive breeding efforts.

Resistance to disease. Hippeastrum or amaryllis mosaic virus and the fungus *Stagonospora curtisii* (red scorch) are the two most serious diseases encountered by amaryllis growers. Viral mosaic symptoms are rarely if ever encountered on plants in the wild. *H. papilio* and *H. reticulatum* do not manifest foliar symptoms as readily as other species and hybrids, but this is no guarantee of actual resistance. However, Williams (1982) has observed that grayish-waxy (glaucous) leafed amaryllis species seem to be very resistant to red scorch

infection. I have also noticed this resistance among such species in my own germplasm collection. Breeding for disease resistance is an area within which much additional work could be accomplished. When growing progeny trials, breeders of amaryllis should be alert for particular crosses or select clones that seem to show resistance to disease problems affecting other progeny.

THE MECHANICS OF BREEDING AMARYLLIS

Pollen collection and storage. All *Hippeastrum* flowers are strongly protandrous, which mean that the anthers shed their pollen before the surface of the stigma is receptive and thus ready for pollination. In the wild, this is a mechanism that helps prevent self-pollination. As the flower begins to open, the anthers are noticeably large and no pollen is visible on the surface. Once the flower is completely open, the anther sacs dehisce, the anthers shrink in size, and yellow pollen is clearly visible on the surface of the anthers (Fig. 1). In most species, the pollen is bright yellow. Pollen should be collected, for immediate use or storage, as soon as the anthers shrink and the pollen becomes visible. Pollen is most effectively stored in size 00 or 000 gelatin capsules, which can usually be purchased from a pharmacy or pharmaceutical supply house. The anthers with exposed pollen are carefully removed from the filaments with a metal forceps, and placed into the longer portion of the capsule. The capsule is put back together, and then should be stored in one of several ways. I prefer to place single capsules in small plastic vials with hinged snap lids. A small amount of desiccant is placed in the bottom 1/4 of the vial, and the capsule is inserted over that. I prefer to use an indicating desiccant (e.g., calcium silicate) that changes color when it absorbs moisture. Additional desiccant is then poured into the vial until the capsule is covered. The vial should then be marked with the name of the plant from which the pollen was taken or by some other system of identification along with the date that the pollen was collected using an indelible felt-tip pen. I also prefer to attach a small string label to the vial with the same information. The vial is then maintained at room temperature for 24 hours, at the end of which time the desiccant is replaced if the indicator dye shows absorption of moisture. The vial can then be placed in the refrigerator or the freezer, depending on how long storage will be required. Alternatively, capsules can be stored together in Mason or other tightly-lidded jars of desiccant. In this latter case, identification should be written directly on the individual gelatin capsules. Non-fat, powdered milk has also been used effectively as a desiccant for this purpose (Bell, 1982).

Pfeiffer (1936) found that amaryllis pollen could be stored for more than 5 months at 50° F and humidity less than 50% and retain germination percentages of 50–75%. If the pollen will be exclusively used during the current flowering season, storage under refrigeration (40–50° F) should be sufficient. If, however, the pollen will be stored until the following year, the vials should be placed in the freezer. I have successfully produced seed repeatedly with one year old pollen that has been frozen since collection.

Anthers can also be collected just before they dehisce, but must then be dried sufficiently before they can be stored. This is best accomplished by placing the immature anthers on a small piece of white paper and placing the paper in a jar or other chamber over a dissident such as calcium silicate. Once the anthers shrink and the pollen appears, the anthers and pollen can be stored as described above.

Determining stigma receptivity. Two different types of stigmas occur in *Hippeastrum.* The most common has three distinct lobes of varying length, while in the other and much more uncommon type, the lobes are largely reduced and the stigma appears round or vaguely triangular. When an amaryllis flower first opens, the style is usually shorter than it will be at maturity and is either declined away from the anthers or held horizontally outward from the flower. The stigmatic lobes remain tightly together. As the flower ages, the style elongates and begins to curve upward (Fig. 2). When the stigma is fully receptive, the style is fully curved upward, the stigmatic lobes are fully expanded and the tiny hairs on the stigmatic surface, called papillae, are clearly visible and upright, giving the stigma a "furry" appearance. If the stigma is not yet receptive, pollen often doesn't adhere very well to the surface. Stigma receptivity is generally reached on the second to third day after the anthers release their pollen, but varies from species to species. As the flower ages further, a bead of viscous fluid may appear on the stigma. Contrary to some observations, when this sticky exudate appears, the stigma is actually past peak receptivity to pollen.

Emasculation and bagging of flowers. Emasculation is the removal of the anthers from a flower scheduled for cross-pollination. It is wise to emasculate any amaryllis flower to which foreign pollen will be applied, even if the plant is known to be self-incompatible. The presence of even a small amount of self pollen on the stigma may induce post-pollination physiological reactions that will prevent any further use of that flower. Enclosing the flower in a paper or light fabric pollination bag after emasculation is anoth-

er precaution against self- or unwanted foreign pollination. However, I have seen no evidence of insect transmission of amaryllis pollen (most species are hummingbird pollinated in the wild), and do not bag the flowers, whether in the field or in the greenhouse.

Pollinating amaryllis flowers. When the stigma is receptive, pollen should be applied to the entire surface of the lobes. If the desired pollen is in short supply, a small brush can be used to pick up pollen from the storage capsule and dust the stigmatic surface. The brush should be carefully cleaned of pollen before making another cross. If large quantities of the desired pollen have been stored, some of the pollen can be poured into the shorter half of the storage capsule or onto a small piece of paper, and the stigma gently dipped into it until it is coated with pollen. If pollen from another plant in flower at the same time will be used, and storage of the pollen is not desired, a stamen can be plucked from the flower of the pollen parent and the anther applied directly to the stigma of the seed parent using the filament as a convenient handle. If the plants are located outside and exposed to rain and wind, enclosing the flower after pollination in a pollination bag will help insure that the stigma remains coated with pollen. The bag can be removed after two days.

Post-pollination phenomena. Within 1–2 days after pollination, the flower will begin to fade. The ovary will begin to noticeably swell between 3 days and 1 week after pollination. If the ovary does not abort by the third week after pollination, chances are good that fertilization has been successful and a capsule will mature. Capsule maturation takes 3–5 weeks on the average, and increases inversely with temperature. During this time the stalk (pedicel) of the capsule will elongate and the ovary will increase 2–3 times in size. When the capsule begins to turn yellow, the seeds are fully mature. Shortly thereafter, the capsule will begin to turn brown and split open into three sections. When the capsule first noticeably begins to turn yellow, it can be enclosed in a bag or a piece of light fabric tied around its base, and allowed to open on the plant. Alternatively, the sealed but mature capsule can be removed and placed upside down in a small paper bag where it will split open within a few days. Amaryllis seeds are black or dark brown, flat, and winged. If an unbagged capsule is allowed to open on the plant, especially a plant in the garden or the field, the seeds can easily blow away.

SEED PROPAGATION AND GROWTH TO FLOWERING OF HYBRID AMARYLLIS

I prefer to air-dry amaryllis seed for one day after harvest and then plant them immediately. Carpenter and Ostmark (1988) found that seed of hybrid amaryllis can be stored for a year at either 11 to 52% relative humidity and 40–60° F without loss of viability. At higher temperatures and humidities, viability loss is rapid. The seed can be sown on any germination medium that drains well but retains moisture, at a temperature between 75 and 85° F, and in about 50% shade. The seeds should be spread across the medium in a single layer and covered no more than 1/8" with medium. The medium should not be allowed to dry out. The first stages of germination (emergence of the cotyledonary petiole) will usually begin within two weeks, while appearance of the first leaf generally takes 4–6 weeks. New seedlings can continue to emerge for several weeks. Seed of some species or hybrids will germinate more rapidly, others more slowly. The seedlings should be pricked out from the germinating pot or flat when one well-developed leaf is evident. A small bulblet will be visible at that time. Seedlings should be shifted to small pots or cell trays of a peat-lite type mix in which they are grown until well-rooted in the cell or pot. In my breeding program at the University of Florida, seedlings are next shifted to 4.5" pots. A sizable number are transplanted into ground beds in the field from 4.5" pots; the balance are transplanted again into 1 gallon containers where they are maintained until flowering. After the initial transplanting into cell trays, a coarser container mix is used for the bulbs (e.g., 40% pine bark, 30% peat, 20% perlite, 10% coarse sand). The amount of shade that the bulbs require is directly proportional to the amount of heat they must withstand; in hot tropical or subtropical climates, 50-60% shade is essential; in milder zones (montane tropics or more northern latitudes), full sun is possible. Amaryllis are heavy feeders and benefit from regular fertilization.

Diploid amaryllis hybrids, especially primary F_1's between species, can flower in 1.5 years or less from seed, though two years is a more reasonable expectation. Tetraploid hybrids may require 2-3 years to reach flowering size.

EVALUATING HYBRID PROGENY

Hybrid populations should be evaluated on the basis of 1) scapes produced per bulb 2) flower number, 3) flower size and form, 4) flower pigmentation and 5) vegetative increase (i.e., number of offset bulbs produced), and any other characteristic desired by the breeder. Occasionally, a diploid cross will

yield one or several tetraploid progeny, probably a result of unreduced gametes in the parents. These may appear larger in all parts than their diploid siblings. It is wise to be liberal when evaluating the first generation of hybrids at their first flowering. At the outset of my own breeding program at the University of Florida, I did not dispose of any of my initial F_1 hybrids until they were evaluated through at least two years of flowering. As the breeder's goals begin to be realized, larger and larger percentages of successive years' progeny will be consigned to the compost pile. The breeder must be heartless; otherwise, he or she is soon overwhelmed by sheer quantities of germplasm. Only superior selections fulfilling a substantial portion of the breeding program's goals will be used in successive generations of crosses.

Breeding after the F_1 generation at the diploid level. It is always desirable to obtain an F_2 generation if possible. It is in the F_2, obtained either by selfing selected progeny or through sib crosses, that assortment of parental characters in various combinations will manifest. Unfortunately, obtaining an F_2 is problematic at the diploid level. With repeated effort, the breeder should be able to obtain some sib crosses among diploid progeny. Successful self-pollination will be, in most cases, restricted to tetraploid hybrids. Complex hybrids between progeny selections from the various F_1 crosses is the most successful strategy for further breeding at the diploid level. If both diploid hybrid parents share one parent species, desirable characteristics of that species will hopefully be dominant. Diploid hybrids of complex parentage [(species A x species B) x (species C x species D)] may show less vigor than the original F_1 parents, as well as lower fertility. These complex second generation hybrids can then be back-crossed to one or both of their F_1 parents. This tact will sometimes restore a measure of vigor and fertility. Finally, F_1 primary interspecific hybrids can be bred to a third species with desired characteristics.

INDUCTION OF POLYPLOIDY AND MUTATIONS IN AMARYLLIS.

As mentioned previously, the self-incompatibility system in diploid amaryllis usually breaks down in tetraploids. Attempts to induce tetraploidy in diploid amaryllis with colchicine have only been sparingly successful. Williams (1982) described a protocol for treating amaryllis seedlings with 0.05% aqueous solution of colchicine mixed with 7 grams per liter of agar. The solution is heated to dissolve the agar and poured off into small containers. Young seedlings (3–4 days after germination) are inverted and immersed into the colchicine gel up to the level just above the roots and left

for 24 hours. They are thoroughly rinsed, then planted in seedling medium. Of those that survive the treatment (colchicine treatments often prove fatal to amaryllis seedlings), some will be induced tetraploids. Unfortunately, using this method I have found that surviving seedlings are usually unstable tetraploids (cells when prepared for chromosome observation show a mix of ploidy levels) and eventually revert to completely diploid. A far more promising method involves using the herbacide oryzalin as a .001% ingredient in sterile medium upon which twin-scale explants are cultured (Van Tuyl et al., 1992). The method has worked successfully on *Nerine*, another member of the Amaryllidaceae. Irradiation of seed or tissue cultured plantlets is another means of inducing both tetraploidy and mutative morphological changes in amaryllis (Kaicker and Singh, 1979), but the necessary equipment is generally unavailable to amateur breeders.

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DEVELOPMENTS IN *HIPPEASTRUM* HYBRIDIZATION, 1799-1999

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THE NATIONAL COLLECTION OF *Hippeastrum*

My interest in *Hippeastrum* began following a visit to the Keukenhof Gardens in Lisse, Holland in Spring, 1993 where, for the first time, I saw a wonderful display of different types of hippeastrums in all shapes, sizes and colors. Since autumn 1994, I have been carrying out research into the history, cultivation and propagation of this plant and have been steadily acquiring more cultivars to grow. Now, less than two years after having become the National Collection Holder for this genus, I have approximately 900 hippeastrums including around 120 complex cultivars of Dutch, South African, North American and Japanese origin; some 15 primary hybrids and over 30 species (mainly from Argentina, Brazil, Peru and Bolivia). Regular trips to Holland since 1997 to visit *Hippeastrum* breeders, growers, and researchers have proved invaluable in enabling me to develop a very detailed knowledge of this genus and to learn about the various processes involved in creating a new cultivar.

REGISTRATION AND CLASSIFICATION OF HYBRIDS

Hippeastrum hybridization began in 1799 when Mr. Johnson, from Prescot in Lancashire, crossed *Hippeastrum reginae* x *H. vitatta* to produce *Hippeastrum* 'Johnsonii'. Since then, the *Hippeastrum* has become very popular with breeders and growers alike. England and Holland became principal centers of breeding activity throughout the nineteenth century when hundreds of hybrids were created. During this period some fine collections were established, only to be abandoned during the 2nd World War when fuel shortages and costs made it impossible for them to be maintained. Such collections included the Westonbirt (owned by Lieut. Col. George Holford), Bodnant, Dell and Exbury. Owners of these collections all developed their own particulaqr strina of Hippeastrum which became well known throuhgout Britain. Other very keen British Hippeastrum enthusaists in the late 19th and early 20th centuries who created some of the finest hybrids of their time included: Normal C Cookson of Oakwood, Wylam and The Right Hon. Lord Rothschild of Tring Park , Hertfordshire. Visitors to the Chelsea Flower Show in London between the two world wars were able to see some

outstanding exhibits of Hippeastrum hybrids which frequently won gold medals and Awards of Garden Merit when exhibited at the Royal Horticultural Westminster Shows in London.

It is unfortunate that so little information about these collections has survived.

During the past 200 years, hundreds of cultivars have been created but, with no registration authority established until 1934 when the American Amaryllis Society was formed, the precise number of cultivars created will never be known. In 1934, Hamilton Traub prepared a listing of only those cultivars that had appeared in major works associated with *Hippeastrum;* this was published in the 1934 Amaryllis Year Book. At the same time, an attempt was made to catalogue all named clones in commercial production.

In 1964 a second catalogue was published as a supplement to Plant Life, vol. 20, entitled: "Catalog of Hybrid Amaryllis Cultivars 1799 to Dec. 31, 1963". As well as including these previous clones, it lists all hybrids registered up until 31 December 1963 and numbers almost 1000 hybrids. Compiled by Dr. Hamilton P Traub, Professor W.R. Ballard, W. D. Morton Jr,. and. E.F. Authement, it can be regarded as the starting point for the nomenclature of hybrid *Hippeastrum.* The majority of hybrids listed in this catalogue were registered between the 1940s and 1963, with a few dating back to the closing years of the 19th century and early years of the 20th century.

Unfortunately very few hybrids developed prior to the late 1950s are still commercially available, but we can certainly get a good idea of their magnificent and regal-like appearance from their descriptive names and physical description. Titles associated with royalty and nobility, such as 'Majesty', 'King', 'Queen', 'Lord', 'Lady' and 'Empress' feature widely, as do names indicating flower color such as 'Cherry Red' and 'Blazing Star' (dark vermilion), both bred by Ludwig & Co. in 1948 and 1958 respectively, or 'Blushing Beauty' (rose pink) created by W.S. Warmenhoven in 1962.

Breeders have always concentrated upon breeding the large flowered hybrids which can usually be classified into one of two categories: Reginae hybrids (Divisions 4A and 4B) and Leopoldii hybrids (Division 5A and 5B). Reginae hybrids have rather drooping, horizontal or slightly upright, moderately open-faced flowers showing the influence of *H. reginae, H. correiensis* and similar species. Petals are broad and overlap to up to 3/4 their entire length. Tips are rounded, sometimes pointed, and the outer edges can be delicately curved and slightly frilly. Petals reflex to a great or lesser extent, depending on the cultivar.

Leopoldii types are similar to Reginae hybrids but with an even flatter, more open face and a tepal tube less than 4 inches long. They derive their name from *Hippeastrum leopoldii* and *Hippeastrum pardinum* which had large blooms with very broad petals, some of which overlapped for almost their entire length. Tips are often rounded with less imbricated types having slightly pointed tips. Flowers are held horizontally and the overall effect is very formal and majestic.

As early as 1934, the Americans recognized the need to establish additional categories to enable other cultivated types to be classified accurately. The result was a total of nine categories including the original two: cultivated wild species (Division 1), long trumpet hybrids (Division 2), Belladonna Hybrids (Division 3), orchid flowering hybrids (Division 6), double hybrids (Division 7), miniature hybrids (Division 8) and unclassified hybrids (Division 9). This system is still used today for formal classification but breeders tend to refer to their creations as being either 'large' or 'small' ("Gracilis"), single or double. However, with the creation of new complex and primary hybrids, some of which are neither large or small, there is a need to review the current system and to create additional categories to accurately reflect these new developments.

In 1980, the Royal Society for Flower Bulb Culture (KAVB), Hillegom, Netherlands (Dutch registration authority for *Hippeastrum*), published the 'Alphabetic List of Amaryllis (*Hippeastrum*) cultivars that are in Cultivation in the Netherlands'. It lists around 230 cultivars, which were being cultivated in Holland at that time.

While the majority listed are Dutch, a few are South African hybrids which were created during the 1960s and '70s by Harry de Leeuw and Floor Barnhoorn (two Dutchmen who left Holland in 1946 to settle in South Africa and set up a business growing a wide variety of bulbous plants including the *Hippeastrum*). Originally known as Harry de Leeuw Ltd, the company is now managed by Floris Barnhoorn (son of Floor Barnhoorn) and his son, Stuart. Since 1980 the company has traded under the name of Hadeco (PTY). Hadeco is now an international leader in the breeding, raising, growing and world wide-distribution of flower bulbs. Hippeastrums are sold as potted plants to many countries throughout the world but particularly in America, Japan and Scandinavian countries. However, the catalogue lists only those hybrids which were in Dutch cultivation at that time and does not pretend to be exhaustive. Others may have been in cultivation at that time, but, as they were not registered, were not included in the list.

Unfortunately, no document listing cultivars registered since 1980 has yet been published, although I understand it is the intention of the KAVB to produce an updated list in due course. With so many developments having taken place during the past 20 years, the need for an up-to-date catalogue is vital. However, of all the hundreds of cultivars that are created, very few are ever registered and therefore have no record (apart from any that the breeder may keep). Some of these unregistered hybrids may be commercially available for a short time, often in very limited quantities, such as the very delicate 'Melusine', while the majority will never make it into commercial production due to a variety of reasons. The exquisite, but unfortunately fungal and disease-prone 'Starry Eyed' ('Spotty' as it was sometimes called, Fig. 1) made a very brief appearance, but due to repeated crop failure because of nematode attack, it was soon discontinued and is no longer cultivated. Sadly, with no information regarding the breeder's name, the plant's parentage and physical description being available, it was as if it 'Starry Eyed' never existed. However, it was, without doubt, one of the most beautiful and exotic cultivars I have ever grown. [Editor's Note: this cultivar is believed by many to be a form of *H. pardinum*].

20TH CENTURY DEVELOPMENTS

The second half of the century was a period of significant breeding developments. Dutch breeders continued to dominate European developments, while South African, Japanese and American breeders played an increasingly important role during the final 30 years.

1940–1969

Dutch developments. With the end of World War II, interest in breeding and cultivating *Hippeastrum* revived, resulting in many new and exciting hybrids. In addition to some magnificent red cultivars (from deepest burgundy to vivid scarlet), a fine assortment of pink, orange and white hybrids, as well as picotee types (white with a red edging) emerged; some combined two or more colors (usually orange or red with white) to produce a most stunning effect. There was much greater variation in size, shape and design than in previous years. In addition to the very large, flat-faced leopoldii types that dominated developments, smaller, more delicate hybrids, known as "Gracilis" because of their graceful appearance, began to appear. However, these did not catch on during this period or become widely available. Some cultivars had distinctly rounded flowers, while others were more triangular or rectan-

gular. Without doubt, the 1960's were a period of great significance in *Hippeastrum* breeding. Principal breeders were Ludwig & Co., G.C. van Meeuwen, W.S. Warmenhoven, Meyers-Mense and van Waveren.

It is regrettable that apart from 'Appleblossom' (Ludwig & Co., 1954) and 'Red Lion' (M. van Waveren, 1958) very few old cultivars of this period are commercially available. Thus, breeders' catalogues and other printed materials describing these cultivars are valuable sources of information.

In 1999 I was fortunate to be given some gorgeous old cultivars including 'White Equester III' (W S. Warmenhoven, 1950's), 'Royal Velvet' (M. van Waveren, 1956), 'Royal Ruby' (W.S. Warmenhoven, 1959), 'Royal Dutch' (Ludwig & Co., 1961; Fig. 1) 'Scarlet Globe' (M van Waveren, 1962) and 'Beautiful Lady' (Ludwig & Co., 1963; Fig. 2). They are splendid hybrids and just as easy to grow as some of today's cultivars.

During this period, many wonderful large red cultivars were created including over 20 hybrids by Ludwig & Co., Hillegom, Netherlands. Some of their best creations belong to the 1950s and include: 'Ludwig's Scarlet' (1950), 'Wyndham Hayward' (1953), 'Ludwig's Masterpiece' (1954), 'Ludwig's Goliath' (1957), 'Blazing Star' (1958) and 'Fire Dance' (1958). Unfortunately none of these are available in the UK today. Until very recently the only red cultivar available in the UK was 'Red Lion' (M. van Waveren, 1958), the oldest, and still the most popular cultivar after 40 years.

Of all the very large dark red cultivars, two of my favourites are 'Royal Velvet' with its lovely deep red to purple blooms and the majestic and mysterious, black-currant red 'Rotterdam' (W.S. Warmenhoven, 1962) with its broad, heavily imbricated and slightly pointed petals that project forwards. 'Scarlet Globe' is a most stunning and unusual looking flower; its scarlet red petals are swept back, giving it an almost totally round appearance. The regal 'Elvira Aramayo' (W.S. Warmenhoven, 1962) with its very broad carmine blooms with magenta rose overlay, and the gorgeous dark velvety red blooms of 'Belinda' (G.C. van Meeuwen, 1963) are two other favorites of mine.

Of the various large white cultivars created during this period, some of the finest were created by Ludwig & Co. and W. S. Warmenhoven. Ludwig's white hybrids include. 'Maria Goretti' (1950), 'White Giant' (1954), 'Ludwig's Dazzler' (1957)—a gorgeous snowy white with frilly edged blooms and lime green throat; 'Picotee' (1958)—an elegant and long lasting large, pure snowy white with an apple green throat capable of flowering from small (20-22 cm) bulbs. The blooms are speckled with red dots and outlined with a thin red picotee. 'Christmas Gift' (1959; Fig. 3) and 'Winter Carnival' (1962) are two other fine hybrids.

In the 1950s one of the finest smaller flowering white cultivars was created by W.S. Warmenhoven: 'White Equester III', followed by the much larger and glorious 'Mont Blanc' in 1962. 'White Equester III' is particularly elegant; its attractive brown scapes, each bearing 5-6 snowy white blooms with an intense lime green throat and reddish brown markings on the outer surface near the base of the flower, make this cultivar particularly beautiful. 'Mont Blanc' is a very robust cultivar with magnificent long lasting blooms that often number 5–6 per scape.

Unfortunately few old pink cultivars have survived from the early 20th century apart from 'Appleblossom' (Ludwig & Co., 1954), with its broad dawn pink and white blooms. However, some truly fine pink hybrids were created by Ludwig & Co. during the 1950's and early 1960's including 'Pink Perfection' (1950)—rose opal; 'Dutch Belle' (1953)—rose opal; 'Delilah' (1954)—begonia-pink salmon; 'Miss Margaret Truman' (1954)—porcelain rose; 'Love's Desire' (1954)—coral pink and porcelain rose; 'Pink Favourite' (1958)—camelia rose; 'Ludwig's Ace' (1959)—azalea pink with Delft rose throat and 'Heaven Sent' (1963)—camelia rose. Only 'Dutch Belle' and 'Appleblossom' are still commercially available. 'Telstar' (M. van Waveren, 1962) with its large solferina purple blooms is still cultivated today.

During this period several large multicolored hybrids were developed which featured two or more colors, usually orange or red and white in various combinations. They were particularly stunning and attracted much attention. Noteworthy hybrids of this type included: Ludwig's 'Candy Cane' (1954)—capsicum red with white streaks and edged with white, and 'Peppermint' (1960)—pure white with red streaks on five of the petals; the lowest being pure white. The throat is a beautiful greenish yellow. 'Royal Dutch' (1961)—orient red, scarlet, white and deep lime green with 5-6 blooms per scape, is without doubt one of the finest ever created. 'Streaking Stripes' (1962) is pure white with mandarin red stripes on each petal and 'Happy Memory' (1963) is predominantly capsicum red with white streaks. 'Minerva', bred by G.C. van Meeuwen in 1962, was another fine large red and white cultivar similar to 'Happy Memory'

Three of the finest salmon/orange large flowering cultivars created during the early 1960s that are still available today are 'Beacon' (W.S. Warmenhoven, 1954—salmon and white broad rectangular blooms; 'Rilona' (G.C. van Meeuwen, 1962)—shrimp red, broad and pointed tip blooms combined with soft shades of brown towards the lime green throat, and 'Beautiful Lady' (Ludwig & Co. 1963; Fig. 2)—gorgeous broad, flat faced salmon pink

blooms. Of all the typical *Hippeastrum* colors, the pastel salmon pink and pale orange shades are some of the loveliest, particularly when combined with soft shades of brown, creamy white and green. Such colors gives these three particular hybrids a distinctive charm all of their own.

South African developments. From the outset, the South African *Hippeastrum* isplayed distinctive characteristics compared to its Dutch cousin. Derived mainly from cultivars of Dutch origin as well as from species, the early hybrids were mainly orange/red, bearing medium/large blooms on short stout scapes (37–47cm) from medium size bulbs. Such features were to undergo considerable development and refinement throughout the next 50 years.

By the late 1950's, the first South African hybrids had become available, many in the USA where they proved to be very popular. Outstanding cultivars of this period included 'Zanzibar' (1963, vermilion), 'Safari' (1963, orient red), 'Zulu' (1963, mandarin red), 'Orangedale' (1962, capsicum red), 'Swahilio' (originally offered under the name 'Satsuma' 1963, Dutch vermilion) and 'Africana' (1963, scarlet). 'El Toro' (early 1960s) was particularly successful and was one of the earliest golden orange cultivars. 'Zanzibar' is still a very popular commercial forcing cultivar with large (19 cm) light bright orange red blooms having a greenish center that are beautifully proportioned.

During the 1960s, hippeastrums in various shades of rose/red had become available. Particularly notable hybrids were: 'Coral Seas', 'Red Sails', 'Watusi' and 'Calabash' (old rose), 'Masai' (1969, red and white striped) and 'Barotse' (1969, cherry). Unfortunately most of these early creations have long since been discarded but two are still available: 'Barotse' and 'Masai'.

However, probably the most important development at this time was the breeding of some truly wonderful pink, some of which are still cultivated today. They include:

'Blushing Bride' (1962). The very large, flat faced, rose madder blooms are exquisitely formed with lovely venation and a bright green throat that are borne on short (37cm) stout scapes.

'Summertime' (1964). Of all the pink cultivars, 'Summertime' still remains the most popular with professional greenhouse growers. It is very quick and easy to grow with foliage present at the time of flowering and very short scapes (38 cm). Two scapes are produced from 30–32 cm bulbs and the large blooms (18 cm) are a lovely nyron rose with broad white central stripes and deeper pink markings towards the throat.

'Springtime' (1968). Soft rose pink (rose Bengal) very flat faced hybrid with slightly taller scapes (40 cm) and foliage present at the time of flowering.

1970–1979

Dutch developments. Unlike the 1950's and '60's, few hybrids were registered during the 1970's as interest in the *Hippeastrum* took a sudden nose dive, possibly due to the oil crisis which had a big impact upon the Dutch economy during that period. Principal breeders during the 1970's were G.C. van Meeuwen, Meyers-Mense, W.S. Warmenhoven and Ludwig & Co.

South African developments. The 1970's were a period of great significance for the South African *Hippeastrum*. Hadeco continued to expand its range of hippeastrums, concentrating upon breeding cultivars that produced more scapes from ever smaller bulbs, with more and larger blooms per scape that were better shaped, and longer lasting with improved color. Reliability, ease and speed of growth were also vital factors in their breeding criteria.

Many of the hybrids had very large (up to 21cm diameter) and heavily imbricated, flat, open faced, upward facing blooms, their openness emphasized still further by the reflexing of the petals. Individual petals were often very broad and rounded, sometimes slightly pointed, with delicately curved edges. Some had ear-like projections from the two inner petals and venation was often exquisite, particularly with some of the pink cultivars.

Unlike the Dutch hybrids that are lifted in August and then given a 10–12 week 'cool period' at 13° C (essential for scape elongation and subsequent flowering), cool soil temperatures in the final few months immediately prior to lifting in South Africa are sufficient for development of next season's scape which has reached 20–25 mm by the time the bulb is lifted in May/June.

During this period more outstanding red hybrids were created that included 'Basuto' (1977, currant red), 'Bold Leader' (1977, orient red) and 'Honeymoon' (1977, rose red).

Two of my favourites that were registered in 1977 and are still cultivated today are 'Desert Dawn' a delicate salmon pink (azalea pink) with beautifully proportioned blooms from smaller bulbs (maximum 28-30 cm) and 'Milady'—a large rose Bengal pink with slightly pointed petals that have delicately curved edges

'Tangerine'. One of the finest orange cultivars of the decade which produced up to 3 scapes from very small bulbs, each scape bearing 4 medium size flowers (12–15cm). It multiplied easily and made an excellent pot plant.

Two stunning striped cultivars of this period were 'Cocktail' (1977, signal red with a pronounced greenish white center) and 'Carnival' (1977, orange red with white rimmed petals and greenish white throat). In the same year a most beautiful large snowy white hybrid was launched,

'Wedding Dance', whose blooms reflexed right back giving it a distinctly rounded appearance.

With the seasons reversed in South Africa, these hybrids are easily made available for flowering during the autumn and early winter of the Northern Hemisphere (the Dutch hybrids must be forced for bloom at this season), and therefore make ideal center pieces for both the office and the home, adding great sparkle to gloomy days.

1980–1999

While the 1950–1970's resulted in a wonderful assortment of mainly large flowering Dutch and South African hybrids, the final twenty years of the century has resulted in a complete new product range of hippeastrums of all types, in a glorious range of colors, shapes and designs. As well as Dutch and South African hybrids, Japanese and North American cultivars began to become available in Europe. With many more cultivars now available commercially, interest in the *Hippeastrum* continues to increase, and breeders are encouraged to create even more cultivars that are easy to grow with unusual designs, patterns and color combinations.

A new chapter began in the late 1980's with the appearance of the first double commercial hybrid [Editor's note: double amaryllis were first reported in the 1930's but were not commercialized until recently]. During the early 1990's, some very dainty pale yellow/green hybrids and several small and medium flowering types that displayed far more variety in shape, design and color than earlier creations became available, albeit in very limited numbers initially. The appearance of some very delicate North American orchid and trumpet type primary hybrids at the end of the century heralded another new chapter in *Hippeastrum* breeding.

HYBRIDS OF THE 1980'S AND 1990'S

Creating a new cultivar is expensive and labor intensive, taking around 7–9 years before any it enters commercial production. Of all the many hundreds of plants that the breeder cross-pollinates each year, only two or three new hybrids are likely to satisfy the breeder's stringent criteria and enter commercial production. Some may have a very short life span; previously undetected problems may appear which may make it unrealistic for the grower to continue cultivating that hybrid. Within a very short time the bulb is no longer available.

When the word "hippeastrum" is mentioned today, most Britons immediately think of large brightly colored flowers but few are able to name more

than two cultivars, 'Red Lion' and 'Appleblossom'. However, there is much, much more to this genus than just these two cultivars. During the past twenty years and particularly during the 1990's, considerable developments have taken place resulting in some stunning large and medium-sized doubles, elegant smaller flowering types, as well as even more spectacular and dramatic large singles.

Leading Dutch breeders include G.C. van Meeuwen, Meyers-Mense, Ludwig & Co., Kwekerij Den Oudendam, T. van Hermitage and Penning Breeding, all of whom have produced some of the finest cultivars in recent years. Exciting developments have taken place in South Africa, Japan and North America in recent years.

Some of the most interesting Dutch cultivars created during the past 10 years are those bred by Marko Penning of Penning Freesia B.V. in Honselersdijk. Martien Penning Sr., who started growing vegetable and fruits on a small scale in Honselersdijk, founded the company in 1926. In 1987 the company commenced an hippeastrum breeding program in cooperation with Floralia, the Dutch bulb growers' association. The first hybrid was launched in 1993 and today some 14 cultivars in a wonderful range of sizes, colors, shapes, and designs are available with new ones appearing each year.

Of the 14, two are small flowering, 'Calimero' and 'Fairytale'. Two are medium or 'midi' flowering, 'Floris Hekker' (Fig. 4) and 'Charisma'. The others are large singles comprising deep velvety reds to cerise pinks, warm oranges and more subtle shades which, when combined with some very interesting and novel shapes and designs, result in a most lively and imaginative assortment. Five cultivars from the Penning Assortment were featured in the Hippeastrum Celebration held at the Royal Botanic Gardens, Kew in April 1999: 'Roma', 'Amigo', 'Nagano', 'Floris Hekker' and 'Calimero'. While all attracted a great deal of attention, 'Floris Hekker' was the most popular of all.

LARGE SINGLES

Large singles (Dutch: 16–17 cm and over, South African: over 13 cm) still remain the most popular and the focus of many breeders' attentions. Many are grown to be sold as bare bulbs, some as potted plants, while those with particularly tall scapes are used as cut flowers where their magnificent blooms look absolutely marvellous in large floral displays. While such large blooms are not to everybody's liking, the latest Dutch and South African developments have resulted in some wonderful new cultivars in a wide range of colors, unusual shapes, and exotic designs that are quick and easy to grow.

Below is a personal selection of particularly fine Dutch and South African cultivars created during the past 20 years, all of which feature in the National Collection.

Dutch

'Piquant' (Meyers-Mense, 1980): beautifully proportioned and exquisite flat faced cultivar having four blooms per scape in various shades of pink, red and orange.

'Clown' (G.C. van Meeuwen, 1980): large, robust plant with flat faced, triangular bright orange and white triangular blooms—one of the finest orange and white cultivars available today.

'Susan' (Meyers-Mense, 1980): large rose pink flattish blooms with a lime green throat. (Also sold under various names including 'Rose' and 'Rosy Queen,' none of which are registered names, but do describe the color of the flowers).

'Wonderland' (Kwekerij Den Oudendam, 1985): lovely soft pink and white rounded blooms with a very prominent green throat (Fig. 5).

'Angelique' (Kwekerij Den Oudendam, 1987): 4–6 very large flat faced dusky pink and white flowers born on thick robust scapes.

'Roma' (Penning Freesia, 1993): one of the best deep red cultivars available today, and a significant improvement upon 'Red Lion'. Mostly 2 scapes from 24–26 cm bulbs and usually 4 flowers per scape.

.'Toronto' (Kwekerij Den Oudendam, 1993): another fine, large deep orange/red and white striped cultivar. Its very broad, flat face, rounded and heavily imbricated petals, and tall stout scapes make it a very striking cultivar.

'Athene' (Kwekerij den Oudendam, 1993): delicate snowy white, long lasting blooms with exquisite frilly-edged petals and deep lime green throat.

'Amigo' (Penning Freesia, 1994): carmine red with a small green center, 4–5 blooms (19–20 cm) per scape. This cultivar is particularly suitable as a pot plant and also makes a very good cut flower.

'Ambiance' (G. Van Staalduinen, 1995): 5–6 creamy white blooms with carmine red stripes each side of a thick white central stripe with a delicate red picotee. It is a most beautiful and striking hybrid.

'Matterhorn' (G.van Staalduinen, 1995): a robust plant with 4–6 beautiful snowy white blooms per scape with a delicate lime green throat. This is

definitely one of the finest of all the very large white cultivars available today.

'Nagano' (Penning Freesia, 1995): particularly long lasting salmon-orange blooms with a white center; mostly 2 scapes from 26-28 cm bulbs and 4-5 blooms per scape. This is a most beautiful and striking cultivar, ideal for pot culture.

'President Johnson' (Ludwig & Co., 1995): long lasting, frilly edged and delicately curved snowy white blooms with lime green throat and red picotee. The venation is particularly exquisite and the petals glisten in the sunlight (Fig. 6).

'Solomon' (Penning Freesia, 1998): particularly long lasting salmon blooms with lime green throat and a dark red ring at the base. This most elegant and appealing cultivar produces 2 scapes from small bulbs and four flowers per scape.

'Forza' (Penning Freesia, 1998): slightly smaller, long lasting delicate orange-red blooms (16–18 cm) with a white center. Four to six blooms per scape and mostly two scapes from 26–28 cm bulbs

'Trendsetter' (Penning Freesia, 1998): four to five charming salmon-pink and white blooms per scape. The broad, slightly pointed petals project forward and are most beautiful. Excellent for pot culture.

'Design' (Penning Freesia, 1998): four to five scarlet and white blooms per scape. The beautiful lime green throat and exquisite venation enhance its appearance still further. Very suitable for pot culture.

South African

'Intokazi' (Hadeco, 1980): four snowy white blooms with petals swept back to create a more rounded appearance. Very fast and easy for forcing.

'Candy Floss' (Hadeco, 1980): dark rose pink with a greenish white throat. A very robust cultivar with strong stems and foliage present at flowering time (Fig. 7).

'Miracle' (Hadeco, 1980): cardinal red with a lovely velvety sheen. It is an excellent greenhouse forcer with two scapes from 26–28 cm bulbs and stems produced close together.

'Merry Christmas' (Hadeco, 1981): one of Hadeco's finest red creations in recent years with huge (20 cm) orient red blooms with a velvety sheen and sparkle borne on very short (30 cm), stout stems.

'Double Six' (Hadeco, 1986): so-called because of its six large upward facing blooms per scape. Ideal for early forcing; the two medium tall scapes

(35 cm) are produced almost simultaneously with foliage developing at an early stage.

'Pizzazz' (Hadeco, 1984): gorgeous and very striking bright red, slightly triangular, very upward facing blooms with a white central star (Fig. 8).

DOUBLES

Doubles have been one of the most significant and novel developments within the past ten years and have aroused strong passions among those who have seen them. Some express utter amazement and delight at seeing such fantastic blooms, while others mutter words of disgust and want nothing to do with such vulgar creations. It seems that you either love or loathe doubles—there is no middle ground. Currently a total of around 25 Japanese, American, Dutch and South African doubles in a range of sizes, shapes and colours are commercially available, but some are more difficult to obtain than others. Some are particularly large with individual flowers measuring up to 24 cm in diameter. These can be very heavy with a tendency to droop, particularly when borne on very long pedicels (as long as 9–10 cm). Like many of the large singles, many of the American and Japanese doubles tend to have little foliage present at the time of flowering compared to the South African doubles. As with the singles, the number of flowers per scape varies according to cultivar; some have 5–6 flowers per scape (e.g., 'Double Record': medium, delicate pink and white blooms, edged with a fine deeper pink picotee; 'Pasadena': medium, scarlet and white with lime green throat; 'Andes': medium salmon pink double/semi double; 'Allure': large white and orange; 'Rozetta': large nyron rose and 'Blossom Peacock': medium white and rose (Fig. 9). Others have 3–4, such as 'Snow White' (large pure white) and 'Ragtime' (large orient red). A few often have just 2–3 blooms ('Lady Jane'). Another problem is the significant gap that often occurs between the opening of the various pairs; this is a particular problem for those having 5–6 flowers per scape.

Flowers other than the first pair are often very immature at the time of the splitting of the spathe values (green bracts which protect the developing blooms) and it can take as long as 10–14 days before the second pair is mature. Not infrequently, the third pair fails to reach maturity and dies. Vase life also varies considerably with some cultivars being much longer lasting than others. Growers aim for hippeastrums to last for 10 days as a cut flower, but some double cultivars have a much shorter life span.

A particular characteristic of doubles, whether large, medium or small, is the absence or partial absence of the reproductive organs. Very few doubles have stigmas and therefore cannot be used as seed parents. Some plants have stamens, the number varying among cultivars, plants of the same cultivar, as well as individual flowers on the same scape. Thickened or misshapen filaments are often embedded in thin, distorted, colored leaf-like structures which are situated in the center of the flower. Sometimes stamens are normal and contain pollen, but embedded filaments may sometimes lack anthers or bear deformed anthers containing little or no pollen. Some flowers combine both free and embedded filaments and anthers. Occasionally a flower may have a free style but lacks the stigma. The number of petals and petaloid structures also varies considerably, varying from 6–18 normal petals and from 0–10 petaloid structures. Not only is the number of petals and petaloid structures cultivar-specific, some cultivars naturally being more semi-double than double, but the arrangement varies considerably in some cases, not only between individual flowers on the same scape, but also between scapes and even from season to season. I have had fully double blooms on a plant flowered in winter or spring followed by single blooms on the same plant flowering again a few months later. The variation in the number of petals and petaloid structures, the presence of misshapen parts and the sheer size and irregular appearance of some doubles can certainly detract from the plant's beauty!

'Double Record' was the first American double to be registered in1990 by John Dene. He subsequently created 'Lady Jane' (large salmon pink) and 'Pasadena'. In 1992 the first of several very large Japanese doubles created by the Miyake nursery were introduced: 'Rainbow' with very large delicately curved white and pink reflexed blooms edged with darker pink, and 'Mary Lou', with gorgeous creamy white flowers suffused with pale pink. During the same year, the first small double 'Jewel' (Fig. 10), also bred by the Miyake nursery, was registered. Its small and delicate creamy white, long lasting blooms have narrow pointed petals which project forwards from a long tepal tube, giving it the appearance of a lily more than a hippeastrum. A ring of small red dots line the lime green throat which has a hint of yellow. Like so many doubles, the degree of doubleness varies considerably among individual flowers as well as among plants. Many 'Jewel' hybrids tend to produce either single or semi double blooms rather than pure doubles.

Three more Miyake doubles were registered in 1995: 'Aphrodite' (1995), 'Andes' (1995) and 'Allure'. 'Andes' is a very unusual medium size salmon

Fig. 1. *Hippeastrum* 'Royal Dutch'

Fig. 2. *Hippeastrum* 'Beautiful Lady'.

Fig. 3. *Hippeastrum* 'Christmas Gift'.

Fig. 4. *Hippeastrum* 'Floris Hekker'

Fig. 5. *Hippeastrum* 'Wonderland'.

Fig. 6. *Hippeastrum* 'President Johnson'

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Fig. 7. *Hippeastrum* 'Candy Floss'

Fig. 8. *Hippeastrum* 'Pizzazz'.

Fig. 9. *Hippeastrum* 'Blossom Peacock'.

Fig. 10. *Hippeastrum* 'Jewel'.

Fig. 11. *Hippeastrum* 'Joker'

Fig. 12. *Hippeastrum* 'Christmas Star'

pink/orange double. It tends to have shorter scapes, possibly due to the lack of a well-developed root system at flowering time in some cases. The quality of its blooms varies; some never attain their full color, even when the plant is placed in full sunlight. As is the case with many double cultivars, there is considerable variation among individual plants in overall shape and the number of petals per flower.

As the century drew to a close, yet another three stunning Japanese creations became available: 'Red Peacock' (1996), 'White Peacock' (1997) and 'Blossom Peacock' (1997; Fig. 9). My favorite is 'Blossom Peacock' with its lovely delicate white and pink, long lasting, and well-proportioned blooms. This particular cultivar is much more consistent in its degree of doubleness compared to some others and usually produces normal anthers as well as embedded ones.

'Red Peacock' is a majestic large double but can sometimes be slow to root. It tends to lack all reproductive organs. Of all the latest doubles, 'White Peacock' seems particularly slow to root. A mass of small very delicate wispy white flowers are borne on short scapes.

Very few Dutch doubles have been created by Dutch breeders so far. 'Nymph', a large snowy white with pinkish/brownish streaks, was registered in 1995 by T. van Nieuwkerk, and is gradually becoming available in the UK. Further Dutch doubles will become available during the early years of the new century.

While developments were taking place in Japan and North America in the 1980's, Hadeco was busy developing its first double, using 'Double Beauty', a cultivar from the collection of the American breeder, Mr. Cothran. Like the singles, South African doubles are produced from small bulbs, all borne on short, stout scapes with leaves often present at the time of flowering. With such heavy and gorgeous blooms, the shorter scapes make these plants far more manageable and less liable to topple over.

Today, more than six South African doubles in a range of colors, styles and sizes are available. Like the Dutch, the majority of doubles created so far are large ('Symphony') but in 1993 two medium size ('Sonata') doubles, 'Alfresco' (snowy white, highly floriferous with 3–4 scapes, each bearing 5–6 peony shaped blooms) and 'Joker' (red and white, 2–3 very short scapes each bearing 5–6 flowers, Fig. 11) were developed, as well as a very delicate small ('Sonatini') double named 'Fanfare'. Further exciting Sonatini doubles are being developed and should be available in the next few years.

Doubles currently available include: 'Ragtime' (1988) having huge orient-red, upward-facing blooms borne on short, stout stems reaching just 30 cm. The presence of leaves at the time of flowering gives this cultivar a full appearance. 'Fanfare' is a smaller version of 'Ragtime', and has exquisite, narrow, wavy, pointed petals and a slightly comical appearance. 'Razzmatazz' (1988), is a striking semi-double with red blooms streaked with white. Two other large fine doubles are 'Rozetta' (1987), with very large (22 cm) nyron rose blooms with a greenish white throat and white streaks in the center of the outer petals and 'My Favourite' (1987) with snowy white blooms with reddish/brown streaks. To date, the only pure white large double available is 'Snow White' (1988); its gently curved frilly edged petals that are swept back make this a truly spectacular plant.

As we enter the 21st century, doubles are still relatively unknown in the UK, but arouse considerable interest when exhibited at shows. Their limited availability and high price mean that they still have novelty value, remaining popular and exclusive. With more new double varieties being introduced continuously, only the best varieties will survive. About 6–8 years ago, any double variety was considered good as long as it was double enough. Nowadays, other traits, such as bulb growth, scape length, production of scapes and flowers are becoming more important, and only the best will enter commercial production.

SMALL FLOWERING TYPES

An important development during the past 40 years concerns the creation of smaller flowering types, generally known as "Gracilis" (Dutch) or "Sonatini" hybrids because of their graceful appearance and size. Characteristics of these very delicate and sometimes exquisitely marked hybrids include 2–3 scapes from small bulbs (16–18cm, South African; 22–24 cm, Dutch cultivars), each scape bearing 6–10 (South African) or 5–6 (Dutch) small flowers which, in some cases, can be particularly long lasting. The narrow pointed petals often project forwards and the tips are sometimes slightly reflexed. Another desirable characteristic is, whether South African or Dutch, many of these cultivars produce several leaves (up to nine) at flowering time, which enhances the plant's overall appearance considerably. While the flowers are small (less than 12 cm—Dutch; less than 11 cm—South African), some cultivars, whether Dutch or South African reach 50cm or over – such tall stems being out of proportion to the tiny, delicate and often lily-shaped blooms. Those with very tall scapes and long lasting flowers are ideal as cut flowers.

Fig. 13. *Hippeastrum* 'Lemon Lime'.

Fig. 14. *Hippeastrum* 'Lima'.

Fig. 15. *Hippeastrum* 'Rio'PPAF.

Fig. 16. *Hippeastrum* 'Sampa'PPAF.

Less than 30 of these wonderful, dainty and elegant types have been created by Dutch and South African breeders so far. After the introduction of 'Picture' in 1958 (possibly one of the earliest Dutch "Gracilis" type hippeastrums of the 20th century) by Ludwig & Co., several other very elegant and attractive "Gracilis" cultivars appeared, all bred by Ludwig & Co. These include 'Pamela' (1960), 'Voodoo' (1960), 'Pixie' (1960), 'Melody Lane' (1964), 'Twinkling Star' (1966), 'Decoration' (1967), 'Fire Fly' (1969), and 'Carina' (1970).

Dutch

Of all the early "Gracilis" types, only two have ever become available in the UK, 'Pamela' and 'Voodoo', and then, only through Dutch mail order companies and a few selected retail outlets. 'Pamela' is capsicum red and has particularly fine, delicate thin pointed petals, while 'Voodoo' has scarlet and white star blooms with the most exquisite venation towards the throat. Each scape has 4–6 flowers.

While "Gracilis" types have been around for some time, they have not succeeded in attracting growers' or exporters' attentions to any great extent and therefore little is known about these cultivars outside Holland. During the 1970's little activity took place and it was not until 1980 that three new hybrids appeared, 'Pygmee' and 'Red Riding Hood', both bred by D. J. v. Geest, and 'Stein's Glory' by K.G. Stein & Co. However, during the past 10 years breeders have begun to take a serious interest in breeding smaller flowering forms. An exciting range of both small and medium size cultivars are now becoming available in a wide range of colors and designs.

Cultivars available today include 'Bianca' (Ludwig & Co., 1970): delicate snowy white with an intense green throat, 'Baby Star' (Stapoflor, Lda, 1991): scarlet and white, 'Calimero' (Penning Freesia, 1994): very delicate, fine bright red flowers and 'Germa' (Len Doran, USA, 1995). Unfortunately this cultivar, which is a complex hybrid involving three species (*H. evansiae*, *H. aglaiae* and *H. parodii*) is prone to so many cultural problems that it may well be shortly discontinued. However the tiny and exquisite creamy yellow trumpets borne on slender elegant scapes is a wondrous sight.

'Donau' (Ludwig & Co., 1996) is a slightly larger "Gracilis" with deep pink flowers, usually 6 flowers per scape and rather tall scapes that can topple easily unless supported with a stick. It is the only deep pink "Gracilis" currently available. 'Salmon Pearl' (Ludwig & Co., 1997) is a most elegant tiny salmon orange and pale yellow cultivar that bears more resemblance to species material.

South African

Like the Dutch, in the past 10 years Hadeco have developed an exclusive range of exquisite and delicate smaller flowering types ('sonatini's')in various colors, shapes and designs. Five are currently available and more are planned for the future. Like so many of the smaller flowering cultivars they make ideal table displays when planted three to a pot.are it

'Panatella' is described as a 'miniature' and has more than 6 small bright red blooms per scape that look wonderful when three bulbs are planted to a pot.

'Veneto' (1988) has gorgeous tiny salmon-pink, trumpet shaped blooms (7.4cm) with a yellow/green center borne on unusually tall and very slender scapes (50–60cm).

'Amico' (1990) is another fine dark red. More than two scapes (length: 40cm) are produced from bulbs measuring only 18cm and three from 24–26cm bulbs with four flowers per scape!

'Top Choice' (1992) is similar in style and color to the medium size Dutch hybrid: 'Floris Hekker'. It is highly floriferous with 6–7 small (10cm) flowers per scape and 2 scapes (length: 32cm) from 22–24cm bulbs.

'Piccolo' (1992) with its very small (9.5cm) cerise red and white star shaped blooms, it has an almost impish appearance and is most appealing.

MEDIUM FLOWERING TYPES—DUTCH AND SOUTH AFRICAN

Recently a small number of medium size cultivars are emerging which neither fit into the large or small flowering categories. Classified as 'Midi's by the Dutch and 'Sonata's by the South Africans, some of these cultivars are also very floriferous, having 5–8 flowers (12cm–16cm diameter—Dutch; 11cm–13cm diameter—South African) per scape, while others tend to have the usual four blooms. Leaves are often present at the time of flowering and some cultivars display unusual and exotic markings. Dutch breeders are aiming to achieve 2 scapes from bulbs measuring 24–26cm; South African breeders are aiming for the same performance but from even smaller bulbs, all in the shortest possible time. However, scape production also depends on the period of growth with more scapes being produced when grown for a longer period.

Currently less than seven 'Midi' or' Sonata' cultivars are available—the most outstanding of these being 'Christmas Star' (Hadeco, 1993; Fig. 12); 'Floris Hekker' (Penning Freesia, 1995); 'Charmeur' (breeder and exact registration date unknown but likely to be late 1990s), 'Jaguar' (G. van Staalduinen, 1997).

'Floris Hekker' is without doubt one of the finest medium flowering cultivars developed so far having many desirable features. Bulbs measuring just 22–24cm usually produce two short scapes (30–40cm) and three scapes from 28–30cm bulbs, each bearing 5–6 bright red beautifully proportioned blooms (14–15 cm diameter) which are particularly long lasting when kept in cool conditions (up to 14 days). Such short scapes do not require staking. Frequently the first two scapes appear simultaneously, followed by a third 7–14 days later. Several mature leaves are often present at the time of flowering which create a much fuller effect. Its compactness, ease, speed (plants were in bloom after 4–5 weeks) and consistency of growth, all contributed to making this hybrid the most popular of all those shown at the 1999 Kew Hippeastrum Celebration.

'Charmeur' is also very floriferous, producing 5–6 long lasting lovely rich orange and white upward facing blooms on short brown scapes and 3 scapes from small bulbs.

Of all these medium size cultivars 'Jaguar' is without doubt one of the most unusual in terms of shape and markings. Its exquisitely striped orange, ox blood red, white and green blooms with narrow, slightly wavy petals make it look more like a member of the cat family and its strange shape bears some resemblance to the Brazilian species, *H. papilio*, which is believed to be involved in its parentage.

'Christmas Star' is so far the only medium size flowering cultivar available from Hadeco., It has around 7–8 brilliant fiery red blooms with a pronounced white center per scape and two scapes from 22–24cm bulbs.

The future of "Gracilis" and medium size cultivars looks good with Dutch and South African breeders taking much greater interest in breeding more of these dainty forms that are proving so popular with the public, particularly in Germany. However, growers tend to be rather conservative and therefore it will need breeders to convince growers and exporters of their economic value as they still tend to be regarded as inferior to the large flowering types. However as the assortment increases, it is likely that exporters will become more interested and hopefully, growers will follow, so resulting in these hybrids becoming more widely available.

YELLOW CULTIVARS

The quest to breed a large bright yellow cultivar has been the goal for many breeders on both sides of the Atlantic for the past 30 years or so, but such an achievement has yet to be realised. Today after considerable efforts only four small—medium pale yellow/green cultivars are available: 'Yellow Pioneer' (Charles Cothran, USA,1972); 'Germa' (Len Doran, USA, created in the early 1970's but only registered in 1995); 'Lemon Lime' (Agriom b.v., 1993; Fig. 13) and 'Yellow Goddess' (Amarylliskw L.G. Vreugdenhil, 1994). All cultivars are unreliable in their degree of yellowness—some more cream or lime green than yellow and some display pink flushes as the flower matures or if it is placed outside in strong sunlight, such as 'Lemon Lime'.

Many breeders consider that the maximum level of yellow has now been reached and that future developments will focus upon breeding easier to grow, large flowering cultivars with the color of 'Germa' or 'Lemon Lime'. In South Africa efforts are continuing to create a large deep yellow hybrid—only time will tell if this will ever become a reality.

QUEST FOR A NEW LARGE RED HYBRID

Despite having been created more than 40 years ago, 'Red Lion' (1958) still tops the charts as being the most popular of all Dutch red Hippeastrums available today. However, it is unreliable, often only producing 2 or 3 flowers per scape instead of the minimum four which is the requirement of those cultivars grown to be sold as potted plants or cut flowers. So the search continues to produce a superior large red. Breeders are confident that such a hybrid can be achieved—it is only a matter of time. If it is to topple the number one, it will have to display significant improvements as regards bulb growth; number and length of scapes; vase life and resistance to certain diseases and these are not easy to achieve.

Apart from 'Red Lion' several other fine large red Dutch cultivars have been produced since 1980 including: 'Liberty' (Jac Mense, 1980)—flat faced very rich velvety red with beautiful curved petals, 'Red Sensation' (Kwekerij De Oudendam, 1993), a smaller very dark rich red and 'Roma' (Penning Breeding B.V., 1993) but none of these have managed to take the place of 'Red Lion'. When finally, a new potential leader does emerge, both growers and exporters will need a lot of convincing, and extensive marketing will be required if the new cultivar is to be a success.

As regards South African reds, there are no shortage of outstanding large red hybrids available. 'Merry Christmas' is one of the finest large reds ever created and is proving extremely popular.

PRIMARY HYBRIDS

More recently there has been a definite shift to using just species material to create a whole new range of small and very exotic primary hybrids. North American breeders have led the way and one in particular—Fred Meyer of California spent many years creating some wonderful new hybrids which are being propagated exclusively for the next 10 years by Leo Berbee & Zonen, Lisse in the Netherlands. This company was established in 1928 by two brothers: Leo and Piet Berbee who started by buying flower bulbs, forcing them and then selling the flowers. In 1966, Leo Berbee's two sons—Leo and Ruud—took over the business and in 1972 the company took over Ludwig & Co., after which they started breeding Hippeastrum. Today, the company is very active in the breeding of Hippeastrum as well as many other bulbous plants that are forced and then sold as potted plants

Until his untimely death in May 1999, Fred Meyer had produced some

absolutely exquisite small flowering creations including 'Lima' (Fig. 14), a cross involving *Hippeastrum papilio* and *H. Cybister* that entered commercal production in Autumn 1998. It is a lime green with beautiful carmine red markings and entered commercial production in autumn 1998.

These new forms are very varied in their shape, design and color and really show the *Hippeastrum* hybrid in a very different light. As a contrast to the very large flowering hybrids, these primary hybrids are exotic and delicate. They display characteristics of both parents and have a wonderful charm all of their own. 'Emerald' has tiny wispy, pale lime green and red flowers with a very thin red picotee; 'Amputo', a small creamy white, has upward facing trumpet shaped blooms. 'Ruby' looks much more like a *Sprekelia* with its beautiful thin ruby colored and yellow blooms.

Unlike the large hybrids, these primary hybrids can be slower and more difficult to grow and require special attention. Root growth can be poor, sometimes not even appearing until after flowering! Scapes can sometimes be short, weak and liable to collapse easily, while others appear to be particularly susceptible to fungal and viral attack. Foliage is often absent at the time of flowering and can be very slow to appear. Flower life can be very short, just 3–4 days in some cases. However, in spite of this, these latest creations are most beautiful and are a most important development in the history of hippeastrum hybridization.

Another American who was very active in *Hippeastrum* breeding during the 1960's—1970's was Len Doran. He was responsible for creating 'Pink Floyd' (1996), a small, very elegant, rose pink, cream, and white trumpet, and 'Jungle Star' (1999), lime green with carmine red markings similar in form and color to 'Lima'. Both are available commercially, albeit in very limited numbers at the moment. Unlike 'Lima', 'Jungle Star' is particularly robust having tall and as many as four scapes from 32–34 cm bulbs, each bearing 4–5 flowers.

Three triploid *Hippeastrum* hybrids bred by Alan Meerow, 'Bahia', 'Rio' (Fig. 15) and 'Sampa' (Fig. 16) are currently being patented by the University of Florida. 'Sampa', a semi-dwarf, produces as many as 8 flowers per scape; 'Rio' is a deep cerise pink with silvery-white keels and intense fragrance, while 'Bahia' is an intense red and white, with a crystalline quality to the flower. All three have *H. papilio* in their pedigree.

FUTURE FOR THE HIPPEASTRUM

Until now, the UK market has been dominated by the large Dutch hybrids and very few people have ever seen the stunning and very beautiful South African cultivars, let alone the Japanese and North American doubles and primary hybrids. In my role as custodian of the National Collection of *Hippeastrum* in Great Britain, I hope to have the opportunity to introduce many of these wonderful hybrids to the British public and help increase the interest and knowledge of this most wonderful plant still further.

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HYMENOCALLIS HENRYAE, A RARE ENDEMIC OF THE FLORIDA PANHANDLE

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Hymenocallis henryae is a rare and enchanting spider-lily species endemic to four counties, Liberty, Gulf, Bay and Walton, of the south central Florida panhandle. The species is remarkable in its characteristics, and it is therefore fitting that it has as its epithet the name of its remarkable discoverer, Mary Gibson Henry (1884–1967), a fearless explorer of the North American wilderness and an internationally renowned field botanist, grower and recipient of the 1950 Herbert Medal (Henry, 1950).

Following US Route 98 along the Gulf coast of the Florida panhandle, Mary Henry was thrilled to discover an unusual *Hymenocallis* in the pine flatwoods just north of Santa Rosa Beach. Its leaves were erect, narrowly strap-shaped, and shiny green. Believing she had found a new species, she sent a collection to Dr. Hamilton P. Traub, a taxonomic authority on the Amaryllidaceae (Traub 1962, Smith & Flory 1989, 1990). Traub grew these plants until they flowered. To his amazement, the perianth rays, as in *Hymenocallis palmeri* S. Watson, were pale green, contrasting beautifully with the snowy white staminal cup (Fig. 1). Wanting to confer a special name on this unique species, Traub chose *Hymenocallis henryae* in honor of its discoverer. The label of Traub's type specimen states, "enchanting species with white staminal cup, green rays" (Traub 1962).

Smith and Flory (1989, 1990) first reported field data on the morphology and ecology of *Hymenocallis henryae*. Dr. Robert K. Godfrey initiated that study in 1986 when he sent to Smith and Flory a bulb sample of his collection No. *82044*. The Smith and Flory study also confirmed the chromosome number of $2n = 38$ and karyotype of *H. henryae* that had been determined by Schmidhauser (1954) and reported by Flory (1975, 1976). In the present study we again confirm the chromosome number and karyotype (Fig. 2).

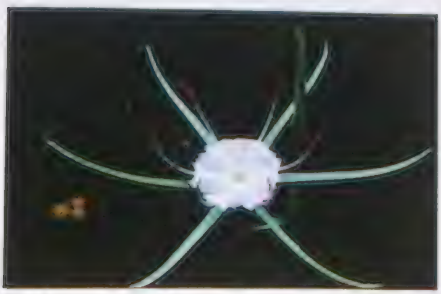

Fig. 1. Strikingly beautiful flower of *Hymenocallis henryae*. (photo by Gary R. Knight)

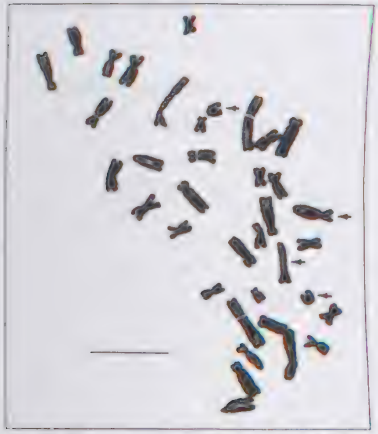

Fig. 2. Chromosomes of *Hymenocallis henryae*, 2*n* = 38. Mitotic metaphase. *Smith & J.de N Henry 1479*. The arrows indicate telocentric chromosomes, and the scale equals 10 micrometers. (preparation by Gerald L. Smith).

In 1989 we studied populations of *Hymenocallis henryae* in both the Appalachicola National Forest, Liberty County, and the pine flatwoods north of US 98, Walton County. Josephine Henry was quick to point out that the heavy glaucescence on the leaves of the plants in Liberty County (Fig. 3) was a characteristic that she did not associate with the shiny leaves of *Hymenocallis henryae* plants in Walton County (Fig. 4). We decided to look for other qualitative and quantitative differences among the populations of *Hymenocallis henryae* throughout its range (Fig. 5). During a ten-year period we gathered morphological data from populations of which we were fortunate to have knowledge (Fig. 6).

Table 1 summarizes the leaf data obtained. We made measurements in the field and grouped the data according to the county in which it was taken. Our sample size represents the number of leaves measured.

Walton County presented a special situation. In our early years of visiting it, one of our sites from which we made a significant number of measurements was undisturbed. However, this site suffered considerable disturbance in the mid 1990's from the logging of the canopy, the clearing of the groundcover, and the rutting of the soil by heavy equipment. In Table 1, we present measurements for Walton County in two categories, before this disturbance and after disturbance.

When the four county data sets of leaf dimensions were used the analysis of variance (ANOVA) showed significant statistical differences

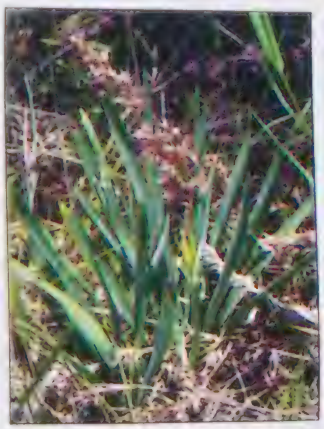

Fig. 3. Glaucous leaves of *Hymenocallis henryae*. (photo by Betsey W. Davis).

Fig. 4. Shiny leaves of *Hymenocallis henryae*. (photo by Susan P. Treadway).

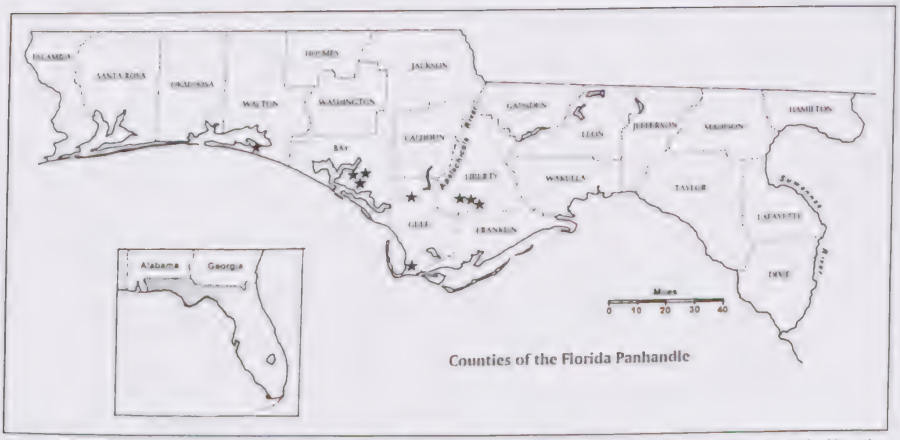

Fig. 5. Distribution of *Hymenocallis henryae* in the Florida panhandle. Map from A. F. Clewell, *Guide to the Vascular Plants of the Florida Panhandle*, used with permission of Florida State University Press.

among the means at the .05 level (Table 2). However, the t-Tests between the leaf dimension means of plants from Liberty County and Walton County before disturbance of habitat showed that there were no significant statistical differences between the means (Table 3). Interestingly, t-Tests between the leaf means of plants from Walton County before disturbance and after disturbance showed statistically significant differences (Table 4). We attribute the differences in leaf dimensions to the stressful conditions the plants were subjected to after their habitat was logged rather than to genetic divergence. The canopy and understory had been destroyed as mentioned above, while the ground cover was mired by deep tractor ruts. The *Hymenocallis* plants appearing after the disturbance were fewer and less robust.

We measured the floral dimensions of *Hymenocallis henryae* and ran statistical tests on sepal length, petal length, and perianth tube length. The means were not statistically different among the counties except for sepal length (Table 5). The longest sepals as well as the longest petals were measured from plants in Liberty County. However, we feel that a larger sample size is needed to show more clearly the quantitative trends of the tepals throughout the range of the species. Floral measurements are presented in the composite description below.

Another characteristic of *Hymenocallis henryae* plants in Liberty County is their tendency to occur in dense clumps. Although we have not quantified this characteristic, we have noted that the plants in the counties to the west of the Appalachicola River often occur singly or in small, loose clumps. In addition, a heavy glaucescence on the surface of the leaves appears only in

the plants from Liberty County, causing the leaves to look blue-green (Fig. 3). In contrast, the leaves of plants in Bay and Walton Counties lack heavy glaucescence and appear green (Fig. 4). Plants cultivated in the greenhouse for several years retain these leaf characteristics as new leaves emerge each year, i.e., the new leaves on plants from Liberty County retain heavy glaucescence, while new leaves on plants from western counties remain glabrous or only slightly glaucous. We therefore consider that leaf glaucousness is a genetic characteristic.

On the basis of the leaf surface characteristic especially, and the other mentioned characteristics, we conclude that there is a trend towards divergence of the Liberty County populations from the populations west of the Appalachicola River. We have decided, therefore, to recognize the populations in Liberty County as a new taxonomic variety.

Hymenocallis henryae Traub, Pl. Life 18: 71. 1962. Green spider-lily

Bulb subglobose, non-rhizomatous, 4–7 cm long, 4–6(8) cm wide, neck 4–6 cm long, basal plate 1–3 cm long; tunica gray-brown. Leaves 3–9, narrowly lorate broadly channeled, erect, glaucous to slightly glaucous or nonglaucous, apex subacute to acute, margin hyaline, deciduous, appearing before the flowers. Scape sub-terete, slightly edged, glaucous, 35–70 cm long, 7–17 mm wide; 2 scape bracts not enclosing the flower buds, 4.5–7 cm long, 10–15 mm wide; each flower with a subtending linear-lanceolate bracteole, 3.8–6.1 cm long, 3.5–6 mm wide. Flowers 2(3), rarely 1, opening sequentially, sessile, slightly diverging, mildly fragrant; perianth tube 6–10(12) cm long, 4–7 mm wide; perianth segments spreading, pale green, sepals keeled with distal osmophore, 9.7–16 cm long, 4.5–9.5 mm wide, petals 8.8–12(15) cm long, 5–9(11) mm wide. Staminal cup white, funnelform, gradually spreading, margin irregularly dentate, 3–4 cm long, 5–6 cm wide; free filaments white, slightly incurved, inserted at a sinus of the staminal cup margin slightly incurved, inserted on a flat sinal base, 2.8–4.5 cm long; anthers 1.5–2.5 cm long, pollen yellow; style green in distal half, fading to white proximally, (13)16–20 cm long; stigma capitate, ca. 2

Fig. 6. Josephine de N. Henry (sitting) observing *Hymenocallis henryae* and Melanie Darst (standing) noting plant associates in shrub thicket. (Photo by Gerald L. Smith)

mm wide; ovary oblong to pyriform, 1.5–3 cm long, ca. 1 cm wide; ovules 4–8 per locule. Fruit subglobose, shortly beaked, 3.5–4.5 cm long, 3–4 cm wide. Seeds obovoid, 1.5–2.2 cm long, 1.2–1.5 cm wide. $2n = 38$.

Two varieties are recognized:

1. Leaves nonglaucous or only slightly so; plants growing singly or loosely clumped. ..... 1a. *Hymenocallis henryae var. henryae*

1. Leaves glaucous; plants often growing densely clumped. ..... 1b. *Hymenocallis henryae* var. *glaucifolia*

1a. *Hymenocallis henryae* Traub var. *henryae*.
Representative specimens examined: U.S.A. Florida: Gulf Co: *Anderson 12026* (FSU), *Leeds s.n.* (PH); Bay Co: *Anderson 15530* (FSU), *Knight s.n.* (FLAS), *Shotz s.n.* (FSU), *Smith & J. de N Henry 1659* (FSU, PH); Walton Co: *M.G. Henry 7080* (PH); *Davis & Davis 15616* (FLAS); *Smith & J. de N Henry 1478* (FSU), *Smith & J. de N Henry 1479* (FLAS, PH), *Smith 1496* (FSU), *Smith & Garland 1523* (FSU, HPU), *Smith & J. de N Henry 1660* (FSU, PH), *Smith & Tobe 1701* (HPU); *Smith, Treadway, & Davis* 1731 (Henry Foundation).

1b. *Hymenocallis henryae* Traub var. *glaucifolia* J. de N. Henry & G. Lom. Smith, var. nov. TYPE: United States. Florida: Liberty Co., NW of Sumatra, 10 June 1986, *Godfrey 82044* (holotype, FSU).

Plantae saepe dense caespitosae; folia 4–7, lorata, erecta, aspectu viridi-caerulea e glaucedine densa, margine hyalino, 30–50 cm longa,1.9–2.9 cm lata; sepala saepe longe patentia, usque ad 16 cm longa.

Plants often occurring in dense clumps; leaves 4–7, lorate, erect, blue-green in appearance from heavy glaucescence, margin hyaline, 30–50 cm long, 1.9–2.9 cm wide; sepals often long-spreading, up to 16 cm long.

Paratypes. U.S.A. Florida: Liberty Co., *Anderson 10617* (FSU), *Gholson, Godfrey & Sigler 11822* (Herb. Gholson), *Smith & Garland 1460* (FSU), *Smith, J. de N Henry & Darst 1474* (FSU); *Smith 1492 &1493* (HPU), *Smith, Treadway & Davis 1732* (Henry Foundation).

Hymenocallis henryae var. *glaucifolia* occurs in the Appalachicola National Forest in cypress depressions at the edge of the pine flatwoods or in depressions along the border of cypress domes. Within the cypress depressions, the green spider-lily plants are often found growing in a loose thicket of *Taxodium ascendens* Brongn., *Hypericum* spp., *Clethra alnifolia* L., *Cyrilla racemiflora* L., and *Smilax laurifolia* L. Ground cover associates include species of *Carex, Panicum, Scleria, Eriocaulon,* and *Sarracenia flava* L.

Upon visiting a cypress dome deep in the Appalachicola National Forest one spring after a winter burn, the authors were elated to see *Hymenocallis henryae* var. *glaucifolia* flowering in a ring around the dome. Controlled burns

are considered essential to maintain the conditions needed for the survival of this species, as well as many other ground cover and understory species.

Hymenocallis henryae var. *henryae* is also associated with pine flatwoods. In the northern part of Gulf County, southwest of Liberty County, Dr. Loran Anderson made a collection of *Hymenocallis henryae* var. *henryae* from a disturbed area along a sandy ridge with scrubby growth bordering a pine plantation. In the southern part of the county near the Gulf of Mexico, *Hymenocallis henryae* var. *henryae* has been found growing at the edge of a shallow water-filled ditch between slash pine/palmetto stands and cypress stringers. Plant associates here included *Ilex cassine* L., *Stillingia aquatica* Chapm., *Polygala cymosa* Walt., *Rhychospora* sp., *Aristida stricta* Michx., and *Panicum* sp.

In southern Bay County near Panama City, *Hymenocallis henryae* var. *henryae* occurs at several sites. On Tyndall Air Force Base, the plants were growing in marshy flatwoods under a canopy of stunted slash pines and a shrub thicket of *Hypericum* sp. and *Stillingia aquatica* Chapm. Herbaceous associates included *Iris* sp., *Polygala cymosa*, and *Proserpinaca pectinata* Lam. *Hymenocallis henryae* var. *henryae* has also been found in a cypress depression drainage that is associated with the Calloway Bayou at Springfield. This area undergoes seasonal drying and there was evidence of logged slash pine. Bordering the depression were dense stands of *Sapium sebiferum* (L.) Roxb, the invasive Chinese tallow tree, and some *Cyrilla racemiflora* L. Ground cover associates included *Aristida stricta*, *Rhynchospora perplexa* Britt. ex Small, *Helenium vernale* Walt., and *Xyris* sp.

In Walton County, scattered clumps of *Hymenocallis henryae* var. *henryae* have been observed in pine flatwoods north of U.S. 98. The canopy of areas that had not been disturbed by recent logging consisted of *Pinus elliottii* Engelm., while the understory was dominated by *Ilex myrtifolia* Walt., *I. glabra* (L.) A. Gray, *Hypericum brachyphyllum* (Spach) Steud., *Cliftonia monophylla* (Lam.) Britt. ex Sarg. and *Smilax laurifolia* L. The ground was thickly covered with tufts of wiregrass, *Aristida stricta* Michx. and the leaves of *Hymenocallis henryae* emerged amidst the tufts. Other frequent ground associates were *Rhexia alifanus* Walt., *R. lutea* Walt, *Eriocaulon* sp., *Lophiola americana* (Pursh) Wood, *Lachnanthes caroliniana* (Lam.) Dandy, *Xyris* sp., *Sarracenia flava* L. and *Osmunda regalis* L.

Outside the Appalachicola National Forest and Tyndall Air Force Base, and particularly in Bay and Walton Counties, the habitats of *Hymenocallis henryae* are seriously threatened. The clearing of pine flatwoods and the draining of cypress swamps for commercial and residential development continue at a rapid rate. Logging practices, although less destructive, also

upset the ecology of the habitats and cause a diminution in number and size of *Hymenocallis henryae* and other species.

The Florida Natural Areas Inventory (FNAI) has organized searches for populations and is tracking them in their database. In association with the Conservation and Recreation Lands program of the State of Florida, FNAI has made recommendations to protect populations where possible, and Stephaniie Barrett of the U. S. Department of the Interior has taken steps to provide official listing of *Hymenocallis henryae* as a federally rare and endangered species. These efforts hold promise to preserve and protect one of Florida's most beautiful and rarest floristic treasures.

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THE SEVEN SPECIES OF KWAZULU-NATAL *CRINUM*: A HORTICULTURAL REVIEW

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There are seven species of *Crinum* to be found in KwaZulu-Natal. They are: *C. acaule, C. bulbispermum, C. delagoense/forbesii, C. graminicola, C. macowanii, C. moorei* and *C. paludosum. Crinum acaule* is the only endemic species and its distribution is centered in the coastal north of Zululand. The only species that needs a cold period over winter is *C. bulbispermum,* thus it stands to reason that it has yet to flower for me in Durban's zone 14. An horticultural key to the species follows:

Leaves thickened towards the middle but without a definite midrib. New leaves form every season, leaves pointed, up to 100 mm broad—sometimes wider in cultivated specimens. Bulb large, up to 2 kilograms in size. Old leaves die off to form a pseudo-stem. Flowers white to deep pink and sometimes white/pink with a darker keel. Flowers are spreading, sometimes reflexed, sometimes campanulate. Bulbs found in shady areas from Umzimkulu (Port Shepstone) in the south to Mtunzini (Central, Coastal Zululand) in the north and inland to Nkandla, Ngome and Pietermaritzburg. .....*C. moorei*

Median leaves up to 50mm broad, flaccid, light green, slightly glaucous. Margins slightly ciliate sometimes hairless. Leaves die back in autumn, therefor new growth always ends in a cut-off point Found in Northern Natal and Zululand in pans, ponds and annual streams. Leaves are recurved, not unlike corn/mealies. Often browsed by cattle and goats and therefor difficult to spot.....*C. paludosum*

Leaves stiff, erect, about 10-15 mm broad. Margins finely toothed, teeth somewhat glassy in appearance. Found in coastal dune forest margins in the sandy grasslands from Matubatuba in Zululand and northwards to Ndumu Reserve. The flowers are scented. .....*C. acaule*

Leaves glaucous green, flaccid to semi erect, sometimes appearing as a pseudo stem. Leaves smooth or undulate, ranging in size up to 1800 mm in length (in cultivation) and up to 150mm wide. Found in forest margins or often under shrubbery and trees in fields. Often naturalises in farmland or disturbed areas. Flowers range from pure white to pink and are

often marked with a darker or pink keel. There is a form with a shortened tube, this is a pale flowered form that can produce up to 3 stems simultaneously. .....*C. macowanii*

Leaves grass to dark green, from 300 mm to 1200 mm in length and up to 150mm broad. Flower light to dark pink with a darker keel.....*C. graminicola*

Leaves light to dark green, margins smooth to slightly ciliate, ranging from about 50 mm to 250 mm in width. Flowers light to dark pink, sometimes almost red and with a darker keel. Seed often apple sized and shape, light to dark red in colour. .....*C. delagoense/forbesii*

Leaves generally wider than 50 mm and glaucous, often appearing a bluish gray in color. .....*C. bulbispermum*

Crinum moorei

C. moorei was one of the first Southern African species to be discovered and was described in 1874. Since *C. moorei* produces apomictic embryos (non-sexual embryos derived from maternal tissue and therefore genetically identical to the maternal plant), there have been many false claims to having bred hybrids when in fact those hybrids are simply natural forms of *C. moorei*. As mentioned in the key, *C. moorei* is at best a variable species. I have found that incompatible pollen used on *C. moorei* stimulates the apomictic process. The resulting apomictic seedlings have darker and smaller flowers, which is perhaps why breeders erroneously feel they have a successful cross. Interspecific crosses with *C. moorei* tend to have the same result. Due to apomixis, most crosses that use *C. moorei* as a seed parent will fail.

C. moorei does best in shade, in damp and slightly clay soil. Mine are situated between two periodic runnels and in summer are often thriving in a bed bordering on cloying mud. Plants in bags will flower in their fourth year. A 5 litre bag is about the smallest you should use. I get excellent growth by using a milled pine bark medium, keeping the medium damp in summer and allowing the bags to dry out in winter.

Here in zone 14, they go dormant for about 30 days in the middle to late winter, but are already displaying their lush foliage before the advent of spring. They begin to flower in early summer and by mid-summer the seeds are harvested. Many of the seeds sprout while still in the pod and if left to drop, the cotyledonary petiole rapidly find cracks in which to grow. Seeds take up to 4 years to produce flowers.

From my 100 or so mature bulbs I get about 50 flower heads but only about 150 seeds. I hand pollinate my colony but find that often one or two golf-ball sized seeds fill the pod. Germination is good, as is survival rate. I end up with an almost 100% success rate. Growth is rapid and tennis ball sized bulbs in the second season are the norm.

Crinum macowanii

This is my favorite species. It was first described in 1878. This species has a fairly long period of dormancy that lasts from late autumn to late winter. It is usually the first of my Natal *Crinum* to produce flowers. Larger (2 kg) bulbs produce up to 5 flower stems simultaneously.

The flowers tend to open in the late afternoon and the bees congregate around the partially open buds and force their way inside. Sometimes as many as 20-30 frantic bees are crawling around one head. *C. macowanii* is different from other *Crinum* in that the cream white pollen ripens on the black stamens while the bud is still fairly tightly closed. In order to produce hybrids, I have had to get to the flowers early in their cycle, remove the unripe stamens, and wait a few more days for the flower to open. Only then do I try the pollen from other species (eg., *C. forbesii*). It is one of the easiest *Crinum* to cross. I have had pollen take from three other Natal species.

Since the pollen ripens before the bud opens. and because wind can be the deciding factor in pollination, many colonies are identical in color, shape and form. I have located many colonies in Natal. Some are to be found in harsh, dry soil, others in semi-shade in rich humus. Some are found in roadside gullies where periodic rain floods the riles, others are found high up on road cuttings where the water is, at best, minimal.

Those found near Estcourt are pink in color, whereas those at the cross-roads between the N3 and Greytown are a pure white. The coastal form is found in humus, in about 75% shade and most of the bulbs have pulled themselves down to a depth of at least 200 mm below the surface. Some that were rescued from a housing complex near here were also deeply buried, but those at Mapumulo and Estcourt had slightly more than their necks exposed.

At my mother's house in Eshowe, which borders the local forest, a medium stand of *C. macowanii* is thriving in the banana patch that is shaded by a large *Ficus natalensis*. Hornbills shriek from the branches and I presume one of them dropped the bitter seed collected from nearby. Years later, there is now a clump of *C. macowanii* and the largest is about 2.5 kgs in size.

These are fast growing *Crinum* and a growth rate of 2.5 cm diameter per

year is not uncommon. For the first few years I still water in winter as I find that the bags tend to get too dry and the bulbs begin to shrink.

From my colony of about 90 mature bulbs, I get about 250 flower-heads per season. This translates to about 3000–4000 seeds per season. Germination is about 80% and survival rate is about 70%.

Crinum graminicola

As this is a horticultural and not a scientific review, it is with great reluctance that I am reviewing this species as something separate from *C. delagoense*. Without the aid of a ruler, noting that the only differences are in the shorter peduncle and pedicel can be a confusing task. The ovary beak in *graminicola* (that supposedly does not occur in *delagoense*), can and often does appear!

Crinum delagoense/forbesii

There is controversy as to whether Verdoorn erred in naming this species *C. delagoense* or whether Lindley gave title to a confused issue. There is a narrow form of *C. delagoense* and one must realize that when Forbes stated that he collected the bulb in the Delagoa Bay area, he was most likely using the last civilized point he had visited in 1826. Ingwavuma/Ndumu is only about two days by horseback from Delagoa Bay (Maputo Harbour). He spoke of a light form and a dark form. Both of these forms are to be found in the Northern Zululand area. A friend returned from Mozambique with a light pink form of *C. delagoense* and the vegetative characteristics are identical to that of the Zululand form. Just to make things more interesting, it is now thought that *C. delagoense/forbesii* should be sunk into *C. stuhlmannii*. However, as stated in the beginning of this horticultural review, the final say as to naming is to be left to others.

These *Crinum* do not flower too well. Last year I managed to get about 15 bulbs to come into flower (perhaps they are still too small?), and, from the 15 heads, about 150 or fewer flowers. From these I ended up with 2 seeds from the *C. forbesii* to *C. forbesii* cross, 10 seeds from the *C. macowanii* on *C. forbesii* crosses and about 20 seeds from the *C. forbesii* on *C. macowanii* crosses. Guess which way I am going to cross in future?

This year (1999) they are doing much better. By the end of October I already had over 30 flower stems, ranging from the short dark patalled form to the lanky pale form that is identical to the mid-coastal-Mozambique form.

Crinum paludosum

I must start off by confessing to cheating! My *C. paludosum* are not Natal in origin but are from the Northern Transvaal. Having said that, I have seen (coveted) and photographed *C. paludosum* near the Ndumu gates. The local conservation officer has told me to put my wish-list in writing and perhaps I will get permission to collect some seeds or seedlings from near the gates. Along the Ingwavuma/Kosi Bay road they are sometimes common alongside the periodic pans/marshes that dot the countryside. They are in full flower during the last week of December but by the second week of January the cattle/goats have feasted upon the foliage and flowers. They need a definite drying off period in winter and do best in bog during the growth period. These flowers are also scented like carnations and the nodding floral stems waving above the water, make for an interesting sight.

My bulbs are very small. They are only in their third year so I cannot go into detail about how to get them to flower. All I know is that they do very well in damp soil, like semi-shade and thrive in having a dry period in winter.

Crinum bulbispermum

This *Crinum* is one of the most sought after species. The flowers range from light red to an almost purple-red and often has a darker keel. It can produce up to 3/4 stems simultaneously. It is found in the colder regions of Natal and the first colonies are at Pietermaritzburg (adjacent to the Conservation HQ). Those flowers are a light red in colour but once you reach the uplands of Natal the flowers are almost purple.

Generally, they are to be found in black clay alongside rivers/streams. The bulbs are often deeper than 300mm (12") and relieving the wild of them is an impossible task (not withstanding the fact that if you are caught you end up deeper than the bulbs themselves!).

Bulbs need a definite drying off period, starting from late autumn to early spring. Plant bulbs deeply in heavy soil and feed well during spring/early summer. They come into flower in early summer and before late summer the seeds have dropped and need planting. If grown in bags, tip the bag over in late autumn to allow the bulb to go dormant.

My bulbs are almost all seed stock that I first received in 1993. No flowers to date but the growth is looking good. I received 2 big bulbs of about 300 grams each in 1994 from a friend in the Transvaal. They are still to flower!

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All photographs by Greg Pettit

Fig. 1. *Crinum acaule*

Fig. 2. *Crinum macowanii*

Fig. 3. *Crinum macowanii*

Fig. 4. *Crinum forbesii/delagoense* from Mozambique.

Fig. 5. *Crinum forbesii/delagoense*

A NEW NOTHOGENERIC TAXON: x*CRIMOCHARIS* (AMARYLLIDACEAE)

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Crinum and *Ammocharis* are closely related genera of the Amaryllidaceae, and they have been frequently confused in herbaria as well as in living plants. There are three particular characters which set them apart: 1) Leaves are distichous and biflabellately arranged in *Ammocharis*, while in *Crinum*, leaves are rosulate or distichous, but never biflabellately arranged; 2) Leaves are sheathed at the base in *Crinum* but not *Ammocharis*; and 3) Fruit are partitioned by three shallow furrows in the pericarp in *Ammocharis*, while fruit of *Crinum* lack furrows (Lehmiller, 1992). There is an apparent misunderstanding regarding non-sheathing of leaves at the base in *Ammocharis* (Killick and Condy, 1994). In his presentation of the Genus *Ammocharis*, Herbert (1837) cited: "Leaves vernal, not sheathing" in his formal definition, and he further elaborated that *Ammocharis* differed from *Crinum* by "leaves not sheathing at the base" and other characters. As leaves of *Ammocharis* emerge from the bulb neck, they are initially planar and pressed flush against each other; if they were sheathed, it would be physically impossible for them to be subsequently segregated into the precise distichous and biflabellate pattern which they assume; sheathing would directly interfere with the alternating arrangement necessary to achieve the biflabellate pattern.

The author, having engaged in interspecific hybridization of *Crinum* for many years, expanded the hybridizing program to include attempts at intergeneric crosses with several species of *Ammocharis*. The latter bulbs included *A.coranica* (Ker-Gawler) Herbert from Potgietersrus, Transvaal, South Africa, and *A.nerinoides* (Baker) Lehmiller from Farm Okaseko, Gobabis, Namibia. All attempted hybrid crosses were accomplished inside an enclosed greenhouse, thus avoiding inadvertent insect pollination. The cross pollinations were performed at twilight shortly after anthesis, using fresh pollen from available species in simultaneous bloom. The program commenced in 1991 with *A.coranica*, and flowers of *A.nerinoides* became available in the spring of 1992.

Successful intergeneric hybrids occurred only sporadically. For example, during 1992, when *A.nerinoides* was utilized as the prospective seed parent, only 3 of 14 attempts yielded hybrid seed, but when employed as the pollen

parent, no hybrid seed formed in 48 attempts. Hybrid seed were frequently small spheres (2–3mm diameter) and differed considerably in appearance from non-hybrid seed of the seed parents. Pending germination, hybrid seed were stored in plastic bags along with small amounts of damp peat moss to prevent desiccation.

The program coninues as of this writing. Although many different *Crinum* species and *Crinum* hybrids have been employed in the intergeneric cross pollinations, the only successful intergeneric crosses have involved bulbs of *Crinum* species originating from Namibia (all of the latter bulbs were collected by the author). The following list represents successful intergeneric crosses by year of accomplishment with the seed parent listed first. Those marked with an (*) have flowered. Unflowered hybrids listed possess intermediate leaf characters and differ significantly from the seed parents.

1992:

*1. *A. nerinoides* x *C. lugardiae*
*2. *A. nerinoides* x *C. baumii*

1993:

*3. *C. baumii* x *A. coranica*

1995:

*4. (*A. nerinoides* x *C. baumii*) x *A. nerinoides*
5. (*A. nerinoides* x *C. baumii*) x *C. baumii*
6. *C. rautanenianum* x (*A. nerinoides* x *C. baumii*)

1998:

7. *A. nerinoides* x (*C. baumii* x *A. coranica*)

x*CRIMOCHARIS* LEHMILLER, NOTHOGENUS NOVUS

Bigeneric hybrid between the genus *Crinum* L. and the genus *Ammocharis* Herbert. Type: *A. nerinoides* (Baker) Lehmiller x *C. lugardiae* N. E. Brown, cultivated 1997, Lehmiller 1942 (holotype: TAMU). Fig. 1.

All that can be stated is that the intergeneric hybrids possesses intermediate characters. A general description is not practical; the population is too small. Furthermore, the available hybrids exhibit extreme contrast due to two factors: 1) Size differential—*C .baumii* and *A. nerinoides* are semidwarf

bulbs, and when combined with much larger taxa, the larger bulbs thoroughly dominate the general pattern of the progeny; and 2) Both *Crinum* subgenus *Codonocrinum* and *Crinum* subgenus *Crinum* are represented in the crosses. For example, *A. nerinoides* x *C. lugardiae* has distichous, nonbiflabellate leaves which are sheathed at the base, and its flowers resemble *Crinum* subgenus *Codonocrinum* (Fig. 1). In contrast, *C. baumii* x *A. coranica* has distichous, nonbiflabellate leaves which are not sheathed at the base, and its flowers more closely resemble *Ammocharis* (Fig. 2).

x*CRIMOCHARIS HARDYII* LEHMILLER, NOTHOSPECIES NOVA.

Planta hybrida *Ammocharis nerinoides* et *Crinum baumii* intermedia; folia disticha non distincte biflabellata.

Holotype: *A.nerinoides* (Baker) Lehmiller x *C.baumii* Harms, cultivated 1997, Lehmiller 1943 (TAMU). Fig. 3. (Nothotaxon named in honor of Dave Hardy, former Senior Horticulturist at the National Botanical Institute, Pretoria, South Africa.)

Bulb ovoid, covered with a brown papery tunic, 30–35mm diameter, elongated into a stout underground neck 40–60mm long. Leaves arising before the flowers, not sheathed at the base, linear and arching, distichous but not clearly biflabellate, truncated at the ends except for new leaves which taper to a slender point, weakly channeled, margins smooth, shiny dark green, 110–290mm long by 3–5mm wide. Scape ovoid in cross section, light greenish tan, 80–120mm long; spathe slender, papery at anthesis, 45mm long; pedicels 35–40mm long; perianth tube rust colored, 80–110mm long; buds not inclining or drooping. Flowers 2–8 per umbel, actinomorphic; segments distally recurved, apiculate, inner wider, 48mm long by 7mm wide, outer longer, 50mm long by 5mm wide, white with a pink stripe on the midline dorsal surface; filaments unequal with the inner longer, inner 42–44mm long, outer 38–41mm long; anthers curved at maturity, pollen gray; style weakly capitate, 52mm long. ovary a small swelling, green; Fruit irregular, usually bearing a short apical projection; seeds sporadic, smooth and spherical if viable.

The surprising aspect of x*Crimocharis hardyii* is that it is seed fertile and produces viable offspring on selfing and on backcrossing (Fig. 4). As none of the x*Crimocharis* individuals has offset, this unexpected fertility raises the possibility of potential commercial applications, as x*Crimocharis hardyii* is easily cultivated in a small clay pot, similar to *C. baumii* and *A. nerinoides*. The remaining x*Crimocharis* hybrids have not proved to be seed fertile to date.

Fig. 1. xCrimocharis, *A. nerinoides* x *C. lugardiae*, type specimen, *Lehmiller 1943*.

Fig. 2. xCrimocharis, *C. baumii* x *A. coranica*.

Fig. 3. xCrimocharis *hardyii*, *A. nerinoides* x *C. baumii*.

Fig. 4. xCrimocharis *hardyii* backcross, [*A. nerinoides* x *C. baumii*] x [*A. nerinoides*].

Fig. 5. Interspecific *Crinum* hybrid, *C. baumii* x *C. lugardiae*.

Note: The taxonomic classification of *C. baumii* is currently cloudy. Ribosomal DNA sequencing studies indicate that *C.baumii* is more closely affiliated with *Ammocharis* and *Cybistetes* than with the Genus *Crinum* (Meerow, personal communication). Morphologically, the problematic character which *C.baumii* presents is extremely narrow leaves; are its leaves sheathed or not at the base (Lehmiller, 1997)? Leaves of *C.baumii* are not biflabellate. Hybrids between *C. baumii* and other species of *Crinum* yield non-distichous leaves with sheathing at the base (Fig. 5). More study is necessary.

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Some Bulbous Flora of the Limpopo River Drainage Basin in the Northern Province

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The Limpopo River valley in the Ellisras and Swartwater areas of South Africa comprises various types of arid moorland with *Acacia*, baobab (*Adansonia digitata*) and *Combretum* the dominant trees. The region has sandy and loamy soil as well as quartz ridges. All these habitats are home to a number of rare and spectacular bulbs, particularly among the Amaryllidaceae. The area is subject to prolonged drought interspersed with wet years. Most of the bulbs remain dormant in droughts but produce spectacular displays of flowers after good summer rains. The summer of 1998/99 was an exceptional season with some of the best flowering, particularly among the amaryllids, seen for many years.

One of the most spectacular bulbs in the Ellisras area is the white-flowered *Nerine laticoma* Th. Dur. & Schinz (Figs. 1, 2). The flowers of this species are usually deep pink or cerise. The umbels of flowers are particularly large, the petals veined pink. Some specimens will flower every year between late November and early January if there has been some rain. In years of above average rainfall such as occurred in November and December, 1998, the veld is scattered with their luminous blooms, often interspersed with the cerise heads of *Ammocharis coranica* Herb. (Fig. 3), the creamy spires of *Sanseviera hyacinthoides* and various *Albuca* species. This is one of the most dramatic and unsung flower displays in South Africa and lasts for about a month. *Nerine laticoma* will set copious amounts of seed at these times. Should follow-up rains occur, the seed, which is round and relatively small, will be distributed across the veld by the runoff, which tends to spread widely across the mostly flat terrain.

A peculiar *Dipcadi* species with attractive undulate leaves also grows with *N. laticoma*. It produces leaves and flowers soon after the first good rains. Once it has seeded, the bulb enters dormancy. This species is encountered in small numbers with the *Nerine* populations but is particularly abundant near Alldays, a small town to the east of Swartwater.

The Ellisras area is very rich in crinums, including the rare *C. foetidum* Verdoorn (*C. crassicaule* Baker) and *C. minimum* Milne-Redh. *C. foetidum* is

one of South Africa's most spectacular bulbous plants. Its broad leaves may reach 2 metres in length and the large attractive flowers are borne in dense umbels, but only in years of good rainfall.

C. minimum is South Africa's smallest species, with thin grass-like leaves which render it cryptic in its surroundings. As with *C. foetidum*, populations are small and scattered, despite seemingly ample suitable habitat. *C. foetidum* grows in deep pink or reddish sand usually in lightly wooded *Combretum* veld. *C. minimum* favors arid stony hillsides lightly wooded with *Acacia* and *Combretum* species. Further east the species is found in small numbers growing in deep sand around baobab trees.

Both these *Crinum* species flower during November if rainfall is frequent and substantial. Even in good seasons a small fraction of bulbs flower, particularly *C. minimum*, which in drought years may not even produce any leaves. Both are also unlike most crinums in South Africa, most of which produce large amounts of seed. These two species restrict flowering to years in which the small amounts of seed produced stand a good chance of germinating. The seeds of both are also unusual in the genus. They are distinctly papillose and rugose (Fig. 4) and are capable of surviving for more than one season if conditions are not conducive to germination.

The two species differ in their mechanisms of seed dispersal however. *C. foetidum* seeds usually land in the soft soil around the base of the parent plant (Fig. 5). They are only moved further afield after particularly heavy thundershowers. The huge leaves of this species (Fig. 6), which coil over the ground around the plant, perform a significant function in holding the seeds within their shelter, where they can germinate and grow successfully, with the result that *C. foetidum* is often found growing in small clumps. The thin, grassy leaves of *C. minimum* have no such retentive powers and its seeds are washed some distance from the parent plant after rainfall, such that plants are widely scattered and almost always encountered singly.

C. buphanoides Welw. ex Baker is very widely distributed around Ellisras and is the most common species. A very gracile form of *C. lugariae* N. E. Brit. is also found here but is much less common. Both species respond to the first substantial summer thunderstorms, which usually occur in October and November. They flower every year with particularly good displays when the early summer rainfall is above average. Seed set is always abundant, sometimes with piles of seed of around the parent plant. These are distributed by rainfall. If seeds are set in dry years or if there is a dry period at seeding time in December and January, the majority of seeds shrivel in the sun.

All amaryllids in the Ellisras area are subject to periodic attack by the Amaryllis caterpillar, *Brithys priori* subsp. *pancratii*. In some years when infestations are heavy, most of the leaves, flowers or seeds of the more common amaryllids are destroyed. The destruction also extends to young bulbs since the caterpillars bore right down into the neck of the bulb, destroying them or causing them to rot. Amaryllids growing in small scattered populations such as *C. foetidum* and *C. minimum* are not as susceptible to these pests. Seed of *C. foetidum* are, however, predated by many insects, and this has a significant effect on the numbers of young plants recruited to the population.

The more unusual crinums and nerines make very showy and unusual garden subjects. Unfortunately few are available at indigenous nurseries, but Linda de Luca, a talented grower, is busy with propagation programs at her nursery outside Johannesburg.

Fig. 1. (far left) The rare and spectacular white-flowered form of *Nerine laticoma*, in bloom near Ellisras in December 1998.

Fig. 2. (left) The umbels of this white flowered form of *Nerine laticoma* are particularly large, at least 15 cm in diameter.

Fig. 3. *Nerine laticoma* plants are interspersed with an almost equal number of *Ammocharis coranica*, the seeds of both dispersed by the flow of rainwater across the flat terrain.

Fig. 4. The unusual rugose and papillose seeds of *Crinum foetidum* and *C.minimum*.

Fig. 5. *C. foetidum* (*C. crassicaule* Baker) in fruit. The ripe seed is deposited close to the plant and often germinates in the shelter of the leaves.

Fig. 6. The long, coiling leaves of *Crinum foetidum* may reach 2 meters in length.

All photographs by Laurian Brown

THE HIGH ALTITUDE PINEAPPLE LILY *EUCOMIS VANDERMERWEI*, A RARE ENDEMIC FROM SOUTH AFRICA

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INTRODUCTION AND CONSERVATION STATUS

The essentially South African genus *Eucomis* L'Hérit faces threats from several quarters, most notably from the popular ethnomedicinal use of the bulbs of two species, *E. autumnalis* (Mill.) Chitt. and *E. bicolor* Bak. for pain and inflammation (Watt and Breyer-Brandwijk, 1962; Pujol, 1993). Subsequent pharmacological testing of *Eucomis* plant parts has validated traditional claims of efficacy. Of five *Eucomis* species assayed for anti-inflammatory activity, *E. autumnalis* and *E. bicolor* showed the highest activity, attributed by Taylor and van Staden (1998) to non-steroidal compounds. Their over-use in traditional medicine has seen shortages in the *muthi* markets of Durban in recent years, as well as elevated market prices (Mander, 1998). However, only one of the world's 14 *Eucomis* taxa has the dubious distinction of making it into the **1997 IUCN Red List of Threatened Plants** (Walter and Gillet, 1998). This is *E. vandermerwei* I.Verd., which is therein listed as rare. A reassessment of the conservation status using the new criteria gives the status as critically endangered (CR B1+2cd) given that the isolated populations occupy a total area of less than 10 km^2. Further, the number of locations is decreasing, and the area and quality of suitable habitats is on the decline. This attractive pineapple lily is limited in distribution to high altitudes between 2200 m and 2500 m along the Drakensberg range, in a handful of localities in Mpumalanga (Fig. 1). Unconfirmed reports extend its distribution into the adjacent Free State province (Hilton-Taylor, 1996). Reyneke (1972) ascribed its restricted distribution to the tendency of the species to grow in isolated groups and hence for it to be easily missed by collectors. Perhaps the habitat type itself has not appealed to the senses of collectors. From such sites, three hitherto unknown taxa have fairly recently been collected and subsequently described: *Disa alticola* H. P.Linder, *Khadia alticola* Chess. & H.E.K.Hartm. and *Delosperma deilanthoides* S. A.Hammer. A recent re-survey of populations has been undertaken by the Mpumalanga Parks Board, and has revealed that the six remaining populations are predominately stable, with a total of 2416

individual plants recorded. However, one population of 45 individuals had disappeared. Populations are so situated that grazing, trampling, fire and alien vegetation pose threats to their long term endurance. Plants grow between rock crevices or under overhanging rocks in low pH sandy soil derived from the quartzitic rocky outcrops in which they occur. The outcrops occur on slopes and plateaus on the region's higher peaks, covered with short to low sour montane grassland, delimited by Low and Rebelo (1996) as "north-eastern mountain grassland" (Fig. 2). It is on the predominantly northerly aspects, the hottest and sunniest aspect in the southern hemisphere, that populations are to be found. Rainfall of between 850 mm and 1200 mm falls in the region, with supplementary precipitation provided in the form of frequent summer mists. Associated vegetation includes the shrubs *Helichrysum galpinii* N.E.Br and *Rhus tumulicola* S.Moore, and the herbs *Crassula setulosa* Harv. and *Rumex angiocarpus* Murb. Geophytes present include *Moraea elliotii* Bak., *Gladiolus ferrugineus* Goldblatt & Manning, *Brachystelma coddii* R.A.Dyer and *Haemanthus humilis* Jacq. subsp. *hirsutus* (Bak.) Snijman. Both *Eucomis autumnalis* (Mill.) Chitt. subsp. *clavata* (Bak.) Reyneke and *E. montana* Compton have been found co-occurring with *E. vandermerwei*.

DESCRIPTION

Although not as small as *E. schijffii* Reyneke, plants of *Eucomis vandermerwei* rank amongst the smaller growth forms seen in the genus. The pear-shaped bulbs typically possess a membranous tunic, and reach 65 mm in diameter. Three to six inclined leaves are produced at any one time, each of which is

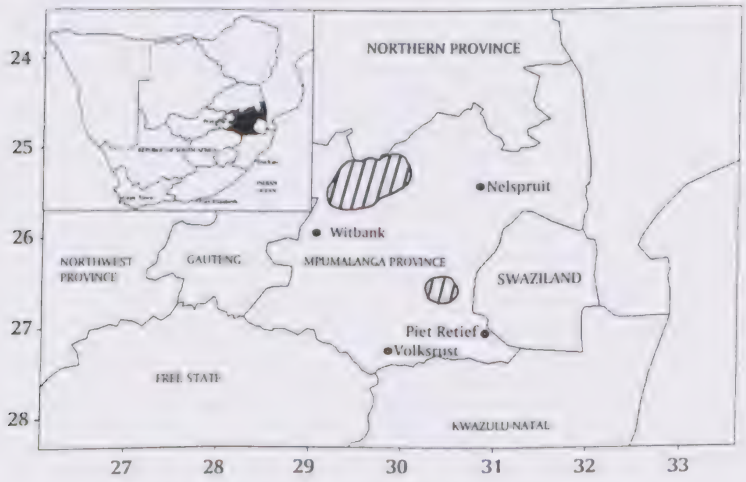

Fig. 1. The distribution of the South African endemic *E. vandermerwei*.

profusely maroon-spotted on the lower half of both surfaces, and more sparsely so towards the apex. Each leaf is strap-shaped with undulate purple margins, between 250 and 500 mm in length and up to 65 mm in breadth. At first glance plants can easily be overlooked as members of another hyacinthaceous genus, *Ledebouria* Roth., the leaves of which are typically spotted and streaked with maroon. However, the presence of a comose inflorescence will quell any doubts in regard to the identity of *Eucomis* plants (Fig. 3). In the case of *E. vandermerwei*, the topping coma hangs prominently over the inflorescence, for each of the bracts are relatively large, being up to 40 mm in length. These 9–15 coma bracts are leaflike in their markings and form, maroon spotted and endued with wavy margins. Similar purplish-brown spotting marks both the raceme, and the slightly clavate peduncle. Inflorescences of *E. vandermerwei* are 20–40 mm in diameter and up to 160 mm in length, with small bracts subtending each flower. These bracts are acuminate in shape, and distinctively saccate near the base. The individual flowers are sub-densely packed, with oblique pedicels 3–6 mm long; perianth segments are green, suffused with purple, 7–10 mm long and 3–4 mm broad, with mucronate apices. The greenish-white filaments, each 4 mm long, unite at the base and fuse with the perianth. The free filament portion is about 4 mm long. The ovary is deeply lobed and purplish, on fertilization developing into a maroon three angled capsule (Fig. 4). On maturity the membrane-like pericarp dehisces, releasing the blackish round seeds, each of which may be 3 mm in diameter. Plants have been recorded as diploid (Verdoorn, 1944; Reyneke, 1972). Populations in the Steenkampsberg flower between November and February, with fruits maturing a month later.

The type collection was made by Dr F.Z. van der Merwe who collected his specimen on the Tautesberg near Middelburg; the specific epithet commemorates his contribution to South African botany, in particular to our understanding of hyacinthaceous genera from the summer rainfall region (Verdoorn, 1944).

CONFUSING SPECIES

Among the short-pedicelled relatives of *E. vandermerwei* (those with pedicels less than 12 mm long), only five possess purple-maroon markings on leaves, coma and peduncle. The tiny *E. schijffii* with its egg-shaped appressed leaves is confined to the Drakensberg of KwaZulu-Natal, the Eastern Cape and neighbouring Lesotho (Reyneke, 1976), while the two subspecies of *E. regia* (L.) Gawl. ex Reyneke occur only in the western Cape (winter flowering with broadly spathulate appressed leaves)(Reyneke, 1972).

E. humilis Bak. and *E. montana* Compton are distinguished in possessing purple rather than greenish-white filaments (Reyneke, 1972). In addition, the coma of *E. humilis* does not overhang the inflorescence, and *E. montana* does not exhibit the localised distribution pattern of *E. vandermerwei* (Reyneke, 1972).

POLLINATION

Flowers typically posses a most unpleasant odor of decaying protein, suggestive of a carrion flower pollination syndrome. As an additional lure to insect pollinators, *E. vandermerwei* offers purple-brown surfaces with a spotted pattern, a feature common to many sapromyophilous plants (Whitehead *et al.*, 1987), and once thought to activate the aggregation instincts of flies, particularly in the presence of putrid scents (Faegri and van der Pijl, 1971). However, in the case of *E. vandermerwei*, flower visitation by carrion insects has not yet been verified by field observations. Whereas deceitful attraction is the rule in sapromyophily, *Eucomis* may be one of a few exceptions for nectar and carrion odour have been shown to be simultaneously present (Pascher, 1959). Faegri and van der Pijl (1971) point out that as many carrion insects place their eggs in dung or carrion but eat carbohydrates themselves, this is not altogether surprising. The co-occurrence of *Brachystelma coddii* (Asclepiadaceae), flowering at the same time, hints at the existence of a small pollination guild operating to the mutual benefit of both plant species. In the cool and often windy population sites

Fig. 2. The natural habitat of *E. vandermerwei*, quartzitic outcrops at high altitudes in mistbelt grasslands of the Mpumalanga Drakensberg. Photograph by N. Crouch.

Fig. 3. Fascinatingly spotted and putridly scented, flowering plants of *Eucomis vandermerwei* are likely to be carrion insect pollinated. Photograph by N. Crouch.

Fig. 4. The maroon three-angled capsular fruits of *E. vandermerwei*. Photograph by S.P. Fourie.

the combined volatiles of a concentrated group of carrion flowers would likely be more attractive to pollinators than would be the scents of isolated individuals. Potential pollinators of such flowers include flies of the families Scatophagidae, Phoridae, and Muscidae, the carrion, dung and saprophytic flies respectively, as well as skin-and-hide (Demestidae) and sap (Nitidulidae) beetles (Whitehead *et al.*, 1987; Scholtz and Holm, 1989). Generalist insect-pollinated plants (entomophilous) such as *Maytenus heterophylla* (Eckl. & Zeyh.) N.K.B.Robson and *Euphorbia clavarioides* Boiss. var. *truncata* (N.E.Br.) White, Dyer and Sloane also occur in the near vicinity, and conceivably contribute towards this guild.

FUTURE PROSPECTS

Efforts to micropropagate *E. vandermerwei* are well advanced (McCartan et al., 1999), providing a protocol for its mass propagation should this species become horticulturally important. In time, cultivation may prove an essential conservation strategy to adopt for this endangered species. For now though, surveys show it to be best conserved *in situ*.

Of its future, who knows? Is this little known pineapple lily yet to yield novel anti-arthritic or pain-killing drugs for mankind, or profit from its horticultural development?

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REPRODUCTIVE BIOLOGY OF *NERINE* (AMARYLLIDACEAE) I: THE ANNUAL GROWTH CYCLE, FLORAL DEVELOPMENT AND GAMETE PRODUCTION

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ABSTRACT

In *Nerine* Herb., the inflorescence is preformed within the bulb scales, two growing seasons prior to flowering. Floral development occurs continuously, encompassing periods of vegetative dormancy, and culminates in gamete production that occurs 4–5 months prior to anthesis. Development within the bud is asynchronous, with florets at different developmental stages present at any one time. This pattern of development renders the inflorescence susceptible to adverse environmental conditions over three seasons; manifestations of disturbance include non-initiation, abortion or malformation of the inflorescence.

INTRODUCTION

Nerine is a genus of mainly autumn flowering bulbs native to Southern Africa. The horticultural significance of *Nerine*, with its colorful, long-lasting blooms, is realized in both cut flower and bulb production. Improvement of horticultural varieties via hybridization began in the mid to late nineteenth century. The first named hybrids, raised by Dean Herbert, were published in Baker's 1888 monograph *Handbook of the Amaryllideae*. The variation present in the genus continues to be recognized by breeders as a source for improved varieties with programs to breed for specific horticultural traits currently being carried out worldwide (Coertze and Louw, 1990; Van Brenk and Benschop, 1993). Information on the reproductive biology and fertility of the genus will assist the success of these programs. This is the first in a series of papers that report on reproductive aspects of the *Nerine* life cycle.

Plants of the genus *Nerine* exhibit one of three basic growth strategies (Norris, 1974): (i) summer dormancy, where leaves emerge after, or concur-

rent with, flowering and persist over winter; (ii) winter dormancy, where leaves emerge in spring and die down after autumn flowering; or (iii) evergreen habit with leaves present throughout the year. Of these, winter dormancy[1] is the most common (Table 1). As with other geophytes, production of food reserves occurs during the active growth period; these reserves can be used to ensure survival during adverse climatic conditions. Although no above ground leaves are present during dormancy periods, the apex remains active and can initiate leaf or floral primordia (Rees, 1989; Theron and Jacobs, 1994; Vishnevetsky et al., 1997).

In *Nerine sarniensis* Herb., autumn flowering is considered to represent the start of a new growing season (Van Brenk and Benschop, 1993), whereas in *N. bowdenii* W. Wats. (also autumn flowering) a dormancy period occurs when the leaves die at the beginning of winter (Systema, 1975). In these two species one growth cycle, consisting of the development of a series of leaf primordia followed by initiation of an inflorescence bud, occurs each year (Rees, 1985; Van Brenk and Benschop, 1993). The number of leaves between inflorescence buds varies between species and cultivars, with 6–8 being usual (Fortanier et al., 1979). The evergreen species, *N. flexuosa* Herb., differs in its growth strategy with the number of leaves between inflorescence buds varying from 3–15 and initiation of buds reported to occur more frequently than once per year (Fortanier et al., 1979).

An unusual feature of *Nerine* is the presence of more than one inflorescence bud in the bulb at any one time and, at least in *N. bowdenii* and *N. sarniensis* , these buds have been initiated one year apart. After initiation, the buds require over 2 years of growth and development before flowering occurs (Theron and Jacobs, 1994; Vishnevetsky et al., 1997). This pre-formation phenomenon has also been reported in another genus of the Amaryllidaceae, *Hippeastrum* Herb., where the time from flower initiation to maturity is 18–24 months (Grainger, 1938). It is yet to be determined how extensive pre-formation is within the family, but extended bud development also occurs in *Amaryllis* L. (12–13 months; Hartsema and Leupen, 1942; cited in Theron and Jacobs, 1994) and *Cyrtanthus* Ait.(Slabbert,1997).

The growth cycle in *Nerine* has been described in *N. bowdenii* (Theron and Jacobs, 1994) and *N. sarniensis* x 'Autumn Glory' (Vishnevetsky et al., 1997). This study confirms and extends their work as well as identifying the timing of gametogenesis in several *Nerine* varieties. The implications of pre-formation are also discussed with regard to horticultural applications.

1. The term dormancy as used here refers to the stage at which no above ground leaves are present.

MATERIALS AND METHODS

All plants used in this study were grown under cultivation at Channel Bulbs, Kettering, Tasmania, Australia. Six randomly selected bulbs of *N. sarniensis* x 'Fothergillii major' and *N. bowdenii* x 'Clone 63' were examined at monthly intervals, for two seasons, to observe initiation and development of inflorescence buds, and to measure the length of the developing bud. In the eight months prior to flowering six randomly selected bulbs of *N. sarniensis* x 'Rosea' were examined on a monthly basis in order to observe the growth and development of the inflorescence. In the four months preceding flowering, bulbs of *N. bowdenii* x 'Clone 63', *N. flexuosa* 'Alba', and *N. sarniensis* x 'Rosea' were also examined to identify timing of gametogenesis.

Buds were prepared for sectioning by fixation in 4% paraformaldehyde, dehydrated through an ethanol series and embedded in butyl methyl methacrylate (adapted from Webb and Gunning, 1990) or glycol methacrylate (Historesin®, Jung) (adapted from Wikeley and Goodsell, 1994). 2µm sections were obtained (Microm 340E rotary microtome) and dried onto slides precoated with 3-Aminopropyltriethoxysilane (Sigma). Sections were stained with Toluidine Blue and examined using a Zeiss Axiovert 35 inverted microscope. Photographs were taken with Kodak Ektachrome 64T Tungsten film.

Bulbs were peeled back to determine diameter at first flowering. This method was also used to identify aborted inflorescences. Number of leaves per growth cycle was counted between inflorescence buds, which could be identified as being one season apart. Mass (fresh weight) of bulbs was determined when in their dormant state, with no above ground leaves present. Bulb unit terminology used in this paper adheres to that of Theron and Jacobs (1994) where each growth unit is represented by an inflorescence bud and a series of leaves. A bud due to flower in the current year is designated as n, a bud due to flower the following year as n+1, and the subsequent year as n+2.

RESULTS AND DISCUSSION

Morphology

Bulbs consist of circular scales, which represent the bases of green leaves. Inflorescences, when present, form between two non-circular scales. Residual flower stalks can be found between outer bulb scales; these together with the outer scale leaves gradually desiccate and are sloughed off. The

minimum bulb mass for first flowering in *Nerine* varies within and between species (Table 2), but it usually represents 4–5 seasons' growth. *Nerine* bulbs must achieve a minimum size before an inflorescence bud is initiated, and a further two growing seasons are required before the bud develops to flowering size. This size (recorded as diameter) is a product of the number of growing seasons and the number of leaves produced each season. Leaf number also varies within and between species, ranging from 3–8 (Table 2). This variation is in agreement with previous studies (Rees, 1985, Van Brenk and Benschop, 1993). It is likely that the variation within species is due, at least in part, to environmental factors as these have been shown to influence the number of florets in a *Nerine* inflorescence (Brown, unpublished).

An irregular number of leaves (4–15) between inflorescence buds has been reported in *N. flexuosa* 'Alba' (Fortanier et al., 1979). This may be attributable to instances where inflorescences have not been initiated due to disturbance or other adverse conditions. Consequently, leaves from two growth cycles will be present between the two remaining inflorescence buds. Inflorescence non-initiation could be expected more commonly in *N. flexuosa* 'Alba' due to its reportedly shorter period of inflorescence development, and the initiation of more than one inflorescence bud in any one year under favorable conditions (Fortanier et al., 1979).

Inflorescence development

A mature bulb of *N. bowdenii* x 'Clone 63' or *N. sarniensis* x 'Fothergillii Major' could contain up to three inflorescence buds at any one time. Both *N. bowdenii* and *N. sarniensis* exhibit an annual growth cycle during which only one bud is inititiated. Timing of inflorescence initiation is similar in both cultivars, occurring in spring (Fig. 1). In *N. bowdenii*, a new inflorescence is initiated during mid-spring (Plate 1a) and two florets in the early stage of development are present by early summer. Initiation of a new inflorescence in *N. sarniensis* x 'Fothergillii Major' occurs during mid-late spring with floral primordia being evident by mid-summer, and floral organs

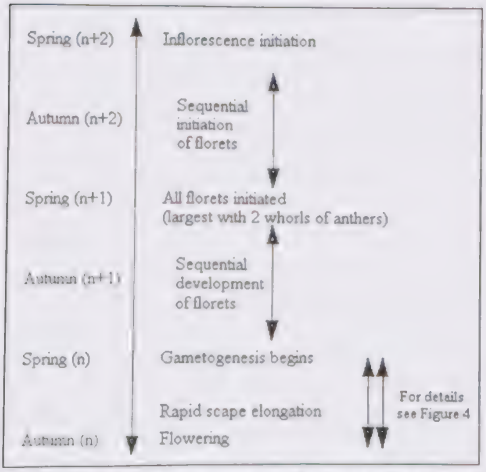

Fig. 1. General development timetable for *Nerine* inflorescence

beginning to develop in autumn. In both species, florets are initiated sequentially and, within each floret, the same pattern of organ development is seen (*i.e.* two whorls of tepals, first whorl of anthers, second whorl of anthers and tri-carpellate gynoecium). Although variation in size of inflorescence buds was found between bulbs, distinct patterns of growth could be identified for the two species.

In *N. bowdenii*, floret development extends over a 32 month period (Fig. 1) and occurs in the three phases outlined by Theron and Jacobs (1994): (i) floral initiation; (ii) floral development; and (iii) floral elongation. However, actual increases in length of the inflorescence bud occur in three separate periods punctuated by two periods where no elongation occurs (Fig. 2). The periods in which bud elongation is absent coincides with dormancy of the bulb. Cessation of any bud elongation during the dormancy periods corresponds with the observations of Systema (1971) who reported that floral buds become dormant as soon as the old leaves die at the beginning of winter. However, while elongation of the entire inflorescence does not occur during this period, differentiation of floral organs is occurring.

Following initiation, the bud gradually elongates to measure approximately 3.5mm (this period is designated I in Fig. 2). A relatively constant length is then maintained during the bulb's dormancy period from May–August. During this first growth season, florets are initiated one at a time until all (usually 4–8) are formed. Development of individual florets proceeds slowly within the bud, continuing over the period when the bud is not elongating. Floret development is not uniform with florets of different stages being present in the same bud (Plate 1b). In winter, at the end of this first season, the largest florets possess two whorls of anthers while the smaller florets only possess tepals and a single whorl of anthers (Plate 1c) or only tepals.

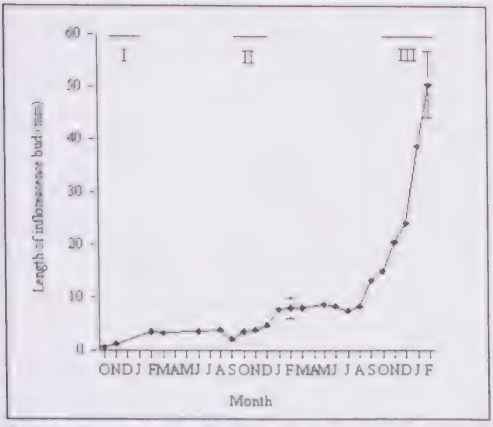

Fig. 2. Growth of inflorescence bud in *N. bowdenii* x 'Clone 63'. I, II, III represent periods of inflorescence elongation.

The second period of bud elongation (designated II in Fig. 2) occurs during the second annual growth cycle, again followed by a suspension of elongation during the dormancy period. Floral organ development occurs in each floret

sequentially and continues through the dormancy period. In autumn, 12 months prior to flowering, the largest florets have formed a tricarpellate gynoecium which is elongating but has yet to fuse. The fusion of the gynoecium is evident in the largest florets from mid-spring with ovules forming in late spring. Gynoecial fusion in smaller florets is completed by mid-summer with ovules forming, after fusion and elongation, in late summer. At the stage of gynoecial fusion, anthers appear to be well developed; however, filaments have yet to elongate.

The final elongation coincides with leaf growth prior to flowering (designated III in Fig. 2) and is longer than the four month period reported by Theron and Jacobs (1994). Initially, growth coincides with spathe elongation, which slows by early summer, remaining approximately the same size for the next three months. Rapid scape elongation occurs during early autumn, immediately prior to flowering, and is accompanied by a further elongation in spathe length as well as the appearance of pigment in the inflorescence. Elongation of individual florets continues after anthesis of the inflorescence, and proceeds rapidly prior to opening. Tepals do not reach maximum length until approximately five days after bud opening.

Unlike *N. bowdenii*, the length of the *N. sarniensis* inflorescence increases gradually and appears to be independent of dormancy (Fig. 3). The inflorescence proceeds through three distinct phases: (i) the first year, where 8–15 florets are initiated sequentially and bud length increases gradually; (ii) the second year, where floral organs are developing, with only a gradual increase in size; and (iii) the final 4–5 months, marked by spathe and scape elongation prior to anthesis (Fig. 3). Inflorescence elongation occurs during all three dormancy periods, with the greatest elongation occurring in the period of dormancy immediately prior to anthesis (Fig. 3).

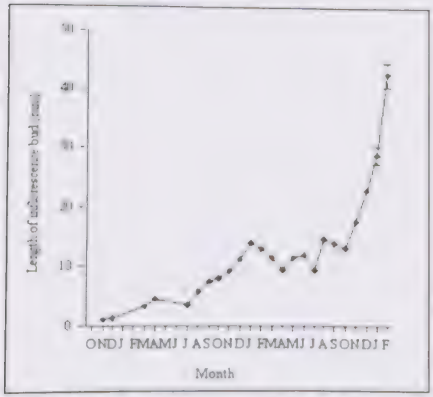

Fig. 3. Growth of inflorescence bud of *N. sarniensis* 'Fothergillii major'.

The pattern of organ development in *N. sarniensis* is sequential and similar to *N. bowdenii*. In winter, at the end of the first season of development, the first whorl of anthers is present in the largest florets. The initiation of the second whorl of anthers occurs in spring of the second season. This is followed by the development

of the unfused tricarpellate gynoecium. Fusion of the gynoecium occurs prior to ovule development, at least in the largest florets. The ovarian cavity is evident from late spring with ovules present in early summer. The ovules arise from the outer wall of the locule and the upper ovules are first to develop.

The observed 32 month period from initiation to flowering in *N. bowdenii* x 'Clone 63' is longer than the 28 months reported for the same species by Theron and Jacobs (1994). Similarly, the 29 month cycle observed in *N. sarniensis* x 'Fothergillii major' is considerably longer than those reported for *N. sarniensis* cultivars by Vishnevetsky and co-workers (1997; 22 months) and Rees (1989; over 18 months, but prior to initiation of a third inflorescence). Climatic conditions, as well as cultivar variation, may account for this discrepancy. As the longer period of development has been observed in this study for two different species, it suggests the Tasmanian climate may be influencing the growth cycles. The scenario of climatic conditions influencing growth phenology and flowering time in *N. bowdenii is* also supported by the work of Shillo and co-workers (1997).

Gametogenesis

In *Nerine*, production of the gametes, the pollen grain and embryo sac, occurs relatively late in the development sequence of the inflorescence. Little previous work has been completed on the timing of gametogenesis in this genus; however, Richards (1990, cited in Theron and Jacobs, 1994) reported that pollen grain meiosis (PGM) occurs during the four month scape elongation period. This study found that PGM occurs during the final elongation period, but it begins earlier than four months prior to flowering, at least in the largest florets of *N. bowdenii* (Fig. 4). This work clearly demonstrates that in all cultivars studied, PGM is not synchronised in the bud. Anthers in smaller florets underwent PGM up to two months after PGM in larger florets. Ovule development and subsequent megasporogenesis/megagametogenesis also

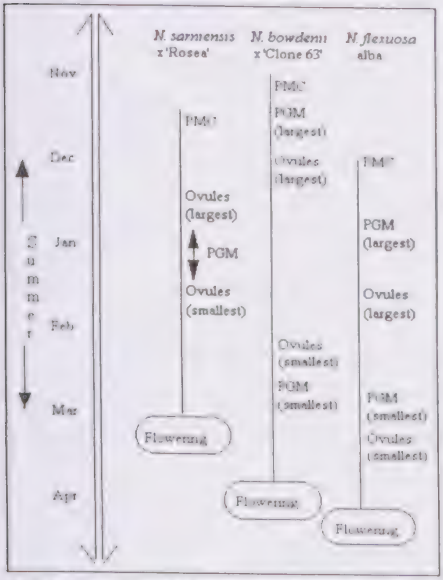

Fig. 4. Gametogenesis development timetable of *Nerine* species. PMCs = pollen mother cells; PGM = pollen grain meiosis; largest/smallest refers to size of floret relative to others in the inflorescence.

are not synchronised within an inflorescence. These processes are sequential, occurring first in the larger florets. Mature embryo sacs were observed at anthesis in *N. bowdenii* 'Clone 63', *N. sarniensis* x 'Fothergillii Major' , *N. sarniensis* x 'Jill', *N. sarniensis* x 'Rosea' and *N. filamentosa*. The egg apparatus is at the micropylar end, with the egg cell positioned slightly above the two prominent synergids (Plate 1d). Megagametogensis in *Nerine* has been described by Amico and Steffanizzi (1980), and is of the *Polygonum* type, commonly found in the Amaryllidaceae (Maheshwari, 1950).

In *N. bowdenii*, pollen mother cells (PMCs) are seen in the first whorl of anthers of the largest florets from early spring (Fig. 4). PGM occurs in these largest anthers during late spring/early summer. Subsequently, pollen grain tetrads (Plate 1e), and released microspores are found. Tetrads in the smallest florets are evident by late summer, at which time unicellular pollen grains, with exine, are present in the largest florets. By early autumn, immediately prior to flowering, all pollen grains have been formed. Ovules form in early summer in the larger florets but are not present in the smallest florets until three months later. Staggered development also occurs in ovules within a single floret. Embryo sac formation is also asynchronous, with the first embryo sacs seen in mid-summer in the largest florets of *N. bowdenii*.

In *N. sarniensis* x 'Rosea', PMCs are found in the largest florets during spring (Fig. 4) and mature pollen grains are present in anthers by mid-summer. Ovules are formed in early summer in the larger florets, while in smaller florets the gynoecium has yet to fuse by this time. Ovules are apparent in smaller florets during mid-late summer, less than one month before flowering. Embryo sac formation occurs first in largest florets and is completed in the smallest florets by anthesis. Vishnevetsky and co-workers (1997) found ovules present in *N. sarniensis* in early summer, which corresponds to these results for the larger florets.

In *N. flexuosa* 'Alba', PMCs are found in the largest anthers in late autumn, with PGM occuring during early summer, and pollen grains present in anthers in late summer (Fig. 4). PGM in the smaller florets occurs in late summer, approximately six weeks prior to flowering. Ovule development in the largest florets occurs in mid-summer but is much later in smaller florets, occurring in the last few weeks before flowering. Megagametogenesis in these florets occurs close to flowering time. Late megagametogenesis is also found in the smaller florets of *N. filamentosa* where embryo sac formation occurs just four days prior to anthesis. At this stage, mature binucleate pollen grains are found in all anthers (Plate 1f).

Horticultural implications

The lengthy period required for initial flowering in *Nerine* is an inconvenience for breeders who need to wait for several years to observe the results of hybrid crosses. Additionally, pre-formation of inflorescence buds has implications for commercial growers. In particular, the inflorescence is rendered susceptible to environmental factors and disturbance over three growing seasons. Interruption in the first season may prevent initiation of the inflorescence, or may affect the number of florets initiated within an inflorescence. In the second season, organogenesis can be affected, while in the third season, gametogenesis, and scape elongation can be affected. Additionally, floral abortion can occur in any of the three growing seasons.

Non-initiation of an inflorescence, found in *N. bowdenii* and *N. sarniensis* (Table 3), is an extreme result of bulb disturbance in the first year of floral development. When this occurs, reproductive effort appears to switch to vegetative propagation; it is not uncommon to observe the initiation of several daughter bulbs after such an event (Plate 1g). This can occur when bulbs are lifted and/or replanted around late spring (*i.e.* the time of initiation). The result of such disturbance is a low flowering percentage in two years. A high incidence of daughter bulb production (with as many as seven per bulb) may alert growers to this situation. Disturbance or adverse growing conditions after inflorescence initiation may cause a reduction in the number of florets in the inflorescence. Variability in floret number within clones of several *Nerine* varieties has been found (Brown et al., in prep.) supporting the possibility that inflorescence modification can be influenced by environmental factors.

Disturbance during the second growth season does not appear to be as critical as in the first season, however abortion of n+1 inflorescences has been found (Table 3). The inflorescence is susceptible to abortion if bulbs are disturbed (*e.g.* lifted and stored) during this second season, especially during mid-late spring (Brown et al., in prep.). As well as time of lifting, storage temperature is critical in decreasing the rate of floral abortion (Groen and Kok, 1997). Incidence of floral abortion in the spathe elongation phase, when gametogenesis is occurring, is low (Brown et al., in prep.). It is probable, however, that observed floral deformities (*e.g.*, short scapes, non-opening florets and empty anthers) can result from disturbance to the bud during this phase. In Tasmania, these deformities were more prevalent during the 1997 flowering season that was preceded by a particularly hot summer.

The late formation of gametes, considering the extensive period of inflorescence development, is an interesting feature of *Nerine*. It may be a func-

tion of the plant not committing resources to a bud that may abort, until it has a reasonable chance of successful flowering. Thus, beginning gamete production during the spathe elongation phase, when the inflorescence has an excellent chance of reaching anthesis, may be of adaptive significance. Progressive and asynchronous gametogenesis may also be an adaptation to ensure that disturbance during development does not affect an entire inflorescence. A short disturbance during the gamete production phase would affect only some of the individual florets and therefore reproductive function, albeit in a reduced capacity, could continue. Observed cases of inflorescences where some florets have empty anthers and others produce normal pollen could be a result of a disturbance to PGM in one floret, with earlier or later PGM in another floret, remaining unaffected.

The pattern of development for *Nerine* inflorescences, in particular late gamete production, needs to be considered by growers. Importantly, bulbs need to be in adequate growth conditions in the 3–4 months prior to flowering. Temperature can be critical with high temperatures during this final phase affecting gamete production. This may be an important consideration in the event of hot summer temperatures. In *N. sarniensis*, gamete production occurs during the dormancy phase of the bulb, so lifting and storing of apparently dormant bulbs at this stage may adversely affect the reproductive capability of the inflorescence.

Plate 1a. Floral primordia of n+2 inflorescence of *N. bowdenii*. Total length = 1mm.

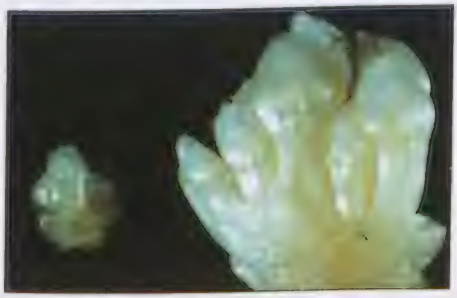

Plate 1b. Inflorescences (n +1 and n+2) of *N. sarniensis* 'Fothergillii Major' in late autumn. Florets at different stages of development can be seen. Largest floret = 9mm.

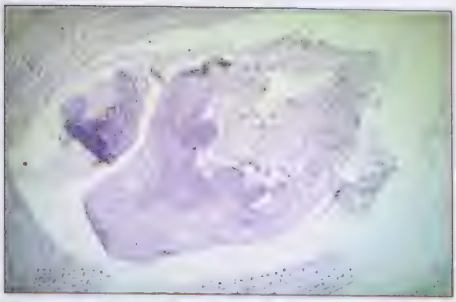

Plate 1c. LS of *N. bowdenii* floret (n+1), showing completely formed tepals and first whorl anther bud. Floret length = 2mm.

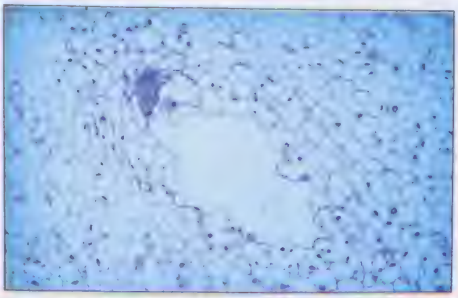

Plate 1d. LS of *N. sarniensis* 'Fothergillii Major' ovule, showing embryo sac with egg cell and two prominent synergids with egg apparatus. Embryo sac length = 380µm.

Plate 1e. Pollen grain tetrads, prior to release from pollen mother cell. PMC diameter = 100µm.

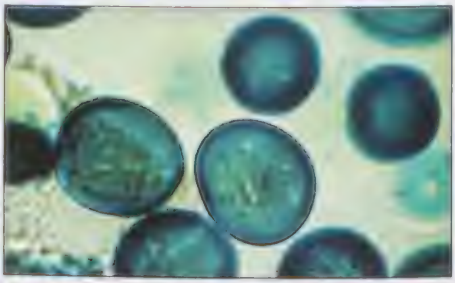

Plate 1f. Mature binucleate pollen grain, showing vegetative and generative cells. Pollen grain diameter = 80µm.

Plate 1g. Bulb of *Nerine bowdenii* with multiple daughter bulbs.

Table 1. Growth strategies of Nerine species (after Norris, 1974; Saunders, 1997).

Summer Dormant	*Winter Dormant*			Evergreen
N. humilis Herb.	*N. appendiculata* Bak.	*N. gracilis* R. A. Dyer	*N. pancratoides* Bak.	*N. angustifolia* Bak.
N. pudica Hook. F.	*N. bowdenii*	*N. hesseoides* L. Bolus	*N. platypetala* G. McNeil	*N. filifolia* Bak.
N. sarniensis	*N. frithii* L. Bolus	*N. huttonii* Shoenl.	*N. rehmanii* L. Bolus ex Traub	*N. flexuosa*
	N. filamentosa	*N. krigei* Barker	*N. transvaalensis* L. Bolus	*N. masonorum* L. Bolus
	N. gaboronensis Bremek. & Oberm.	*N. laticoma* Th. Dur. & Schinz.	*N. undulata* Herb.	
	N. gibsonii K. H. Douglas	*N. marincowitzii* D. A. Snijman		

Table 2. Mass and diameter of (dormant) bulb at first flowering, and average number of leaves present between successive inflorescence buds (range shown in parentheses).

Cultivar	Bulb mass	Diameter	Leaves/growth cycle
N. bowdenii x 'Clone 63'	34g	51±2.0mm	6.3±0.2 (5-8)
N. flexuosa 'Alba'	38g	n/a	5.5±0.5 (5-8)
N. sarniensis 'Fothergillii major'	45g	54±2.0mm	6.2±0.3 (4-8)
N. sarniensis x 'Rosea'	12g	n/a	4.5±0.2 (3-8)

Table 3. Percentage of bulbs where inflorescence is not initiated or aborted.

Cultivar	% non-initiated	% aborted	Total No.
N. bowdenii x 'Clone 63'	15	19	27
N. sarniensis x 'Fothergilii Major'	19	12	26
N. sarniensis x 'Rosea'	6.5	5	54

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Reproductive biology of *Nerine* (Amaryllidaceae) II: Embryo development and seed germination

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Abstract

Nerine Herb. seeds are fleshy, starch rich and do not undergo a dormancy period. A pro-embryo is present at seed shed. Development proceeds in a period of after-ripening and the embryo progresses through a globose stage to a bipolar club shape at maturity. At germination, the embryo remains rudimentary, with no leaf or root structures. Emergence of the cotyledon is followed by formation of a probulb at the distal pole. Subsequent development of a contractile root precedes the appearance of leaves, and acts to pull the probulb into the substrate. The optimum temperature for germination is approximately 20°C. Temperatures of 30°C cause seed degeneration, while temperatures of 10°C and 15°C slow germination rate without affecting seed viability. Storage of *N. bowdenii* W. Wats., *N. flexuosa* Herb. and *N. undulata* Herb. seeds at 4°C suspends embryo growth and prevents germination until seeds are removed from storage.

Introduction

Nerine is a genus of mainly autumn flowering bulbs with attractive, long-lasting blooms prized for bulb and cut-flower production. There are approximately 23 species native to Southern Africa (Snijman, 1995) the habitats of which range from the cool montane environment of the Drakenburg Mountains to grassland and swampy plains (Norris, 1974; Saunders, 1997). Hybridization programs within and between species have been carried out since the mid 19th century (Baker, 1888) and this has resulted in over a thousand named cultivars and many more hybrids used for breeding stock.

The inflorescence of *Nerine* is preformed within the bulb scales, two flowering seasons prior to flowering (Theron and Jacobs, 1994). After the first annual cycle in *N. bowdenii* and *N. sarniensis* Herb., individual florets

of the inflorescence are initiated, with tepals, and at least the first whorl of anthers, formed. The second whorl of anthers follows and, by the end of the second annual cycle, the gynoecium with ovules has been formed. Production of the gametes does not occur until the final months prior to anthesis (Brown *et al.*, 1999). The ovary of *Nerine* is inferior, possessing three locules with a varying number of anatropous ovules present in each locule (Dahlgren and Clifford, 1982). The ovules have a single, multi-layered integument with obvious stomata (Dahlgren *et al.*, 1985).

In *N. bowdenii* and *N. sarniensis*, the process from pollen germination to pollen tube penetration of the micropyle takes approximately three days and fertilization may result from pollinations occurring from anthesis of a floret up to 14 days after anthesis (Brown, unpublished data). The number of seeds produced per capsule varies within and between species, with 1–3 seeds commonly produced. However, seed numbers as high as 25 have been formed in *N. sarniensis* cultivars.

Seeds are large, fleshy, globose to ovoid and are water-rich; the seed of *N. sarniensis* has a water content of 73.8% (Isaac and McGillivray, 1965). This is unusual as many angiosperm seeds are desiccated at maturity, containing only 5-15% water (Bewley and Black, 1994). Furthermore, the seeds are unusual as they possess stomata and contain chlorophyll in the integument. These features are rarely found in angiosperm seeds (Maheshwari, 1950). The presence of chlorophyll in seeds of *Nerine*, as well as the closely related *Brunsvigia* and *Amaryllis*, was first identified by Hofmeister (1861, cited in Maheshwari, 1950). Stomata were first observed in the seed coat of *N. sarniensis* (referred to as *N. curvifolia* by Schlimbach, 1924; cited in Snijman and Linder, 1996) and have since been observed in other species of *Nerine* (Snijman and Linder, 1996; Brown, unpublished). Another characteristic of members of the tribe Amaryllideae that, along with *Nerine*, includes *Amaryllis* L., *Brunsvigia* Heist. and *Crinum* L. (Snijman and Linder, 1996), is the absence of seed dormancy.

Following normal embryo development and gaining an understanding of the ontogeny of the embryo is very useful for plant breeders. This information provides a basis on which to intervene when embryos from hybrid crosses break down prior to germination. This is a common occurrence in wide, inter-specific or inter-generic, crosses (Ladizinsky, 1992). Seed breakdown is usually a result of chromosome imbalances in the embryo or endosperm (Monnier, 1995) and has been encountered in *Nerine* (Brown, unpublished). Comparison of growth between normal and aborting

embryos allows identification of an appropriate stage for an intervention, such as embryo rescue. Embryo rescue has the capacity to save failing hybrid crosses by excising immature embryos from seeds, and aseptically culturing them *in vitro* on an artificial nutrient medium (Monnier, 1995).

Materials and Methods

Plants used in this study were grown under cultivation at Channel Bulbs, Kettering, Tasmania, Australia. *Nerine bowdenii* x 'Clone 63', *N. sarniensis* x 'Rosea', *N. flexuosa* 'Alba', *Amaryllis belladonna* L. and *A. belladonna* x 'Hathor' were grown in the field, while other varieties were grown under plastic tunnels.

Embryo sections were obtained by hand-sectioning seeds or microtome sectioning ovaries/seeds. Hand cut sections were stained with Calcofluor (Calcofluor White M2R) and Acridine Orange (Solvent Orange, Sigma). Microtomed material was fixed in 4% paraformaldehyde, dehydrated through an ethanol series and embedded in butyl methyl methacrylate (adapted from Webb and Gunning, 1990) or glycol methacrylate (Historesin®, Jung) (Wikeley and Goodsell, 1994; D. Wikeley pers. comm.). Small incisions were made into the seed coat to facilitate infiltration of the embedding solutions (M. Sedgley, pers. comm.). Sections were obtained using a Microm 340E rotary microtome, dried onto slides precoated with 3-Aminopropyltriethoxysilane (Sigma) and stained with Toluidine Blue or the DNA fluorochrome Hoechst 33258 (Sigma). The presence of starch was detected by staining with iodine solution. Sections were examined using a Zeiss Axiovert 35 inverted microscope fitted with an HBO mercury vapour lamp. An excitation filter BP365/12, dichroic beam splitter FT395 and barrier filter LP 397 were used for observation of fluorescence. Fluorescence micrographs were taken using Kodak Ektachrome Daylight 200 film; all other photographs were taken with Kodak Ektachrome 64T Tungsten film.

Early embryo size was measured by light microscopical observations of fluorescently stained material. Four weeks after seed shed, embryos were dissected out under a Zeiss Stemi SV stereo microscope into a graduated petri dish. Six to twelve seeds were dissected at weekly intervals; however, in early stages it was not possible to locate embryos in all seeds.

Germination trials were carried out on double sheets of moist filter paper and data were obtained by weekly observation of seeds. Temperature trials used 30 seeds per temperature for *N. bowdenii* and 20 seeds per temperature for *N. sarniensis*. Only viable seed was used in calculations.

RESULTS

Embryo development

After fertilization, approximately three days after pollination, the nuclear endosperm develops with an initial suspension of embryo growth. Significant seed enlargement follows, predominantly due to cell division and enlargement in the multi-layer integument. At seed shed, a spherical pro-embryo, measuring 100–150µm, with a clearly visible suspensor is present at the micropylar end of the embryo sac (Plate 1a). The endosperm surrounds the embryo at this stage; however, it contributes a small proportion (<5%) of the actual seed volume. The ontogeny is similar for all species studied, starting with a pro-embryo and continuing development after seed shed. However, the speed of development varies between species and is reflected by the differences in the timing of seed shed and subsequent germination (Table 1). The timing of developmental processes subsequently referred to is for *N. bowdenii* and is outlined in Table 2. Embryo size was measured at weekly intervals in *N. bowdenii* and is illustrated in Figure 1.

During the first two weeks after seed shed (W5[1]–W6) the developing embryo becomes globose and occupies the width of the embryo sac. The suspensor cells are still evident and the basal cell has undergone division (Plate 1b). At W6, the embryo is approximately 0.1mm in length and difficult to locate within the large seed. Polarity is evident at approximately W7, when the embryo assumes an almond shape. At these initial stages, there is little external or internal differentiation. By W8, embryo length is approximately 0.9mm; at this stage an embryo can be excised with the aid of a dissecting microscope.

Differentiation becomes evident at W9, with the appearance of a distinctive epidermis in longitudinal section. The two poles of the embryo curl around forming a crescent shape, with a bulge developing in the center (Plate 1c). The cells in this central bulge are much smaller than surrounding cells, suggesting they are rapidly dividing. During the next two weeks, a girdle of meristematic cells around the outside of the embryo becomes apparent. This coincides with the beginning of a period of rapid elongation of the embryo that has now assumed a club shape (Plate 1d).

Elongated procambial cells are apparent in longitudinal section at W10 (Plate 1d). Significant meristematic activity and cell differentiation also occur in the region that will emerge from the seed. Elongation and expan-

1. Time; W0–W17 refers to weeks after anthesis of the floret, (outlined in Table 2).

sion of the embryo continue until germination occurs in the following 2–3 weeks. The embryo remains small and uncoiled, occupying less than 10% of the seed volume at germination.

At germination, which occurs in close proximity to the hilum, a tubular, non-chlorophyllous cotyledon emerges having a sheath-like, protective cap of cells at the tip. In cross section, embryonic leaves are seen in the region below the tip (Plate 1e). The shoot apex is externally visible as a small notch, which is in close proximity to the emerging tip. The cotyledon is positively geotropic while the radicle pole undergoes swelling to form a probulb. A contractile root emerges from the probulb and develops into the major root during the first growth season (Plate 1f). Its contractile properties act to pull the young probulb down into the substrate. The cotyledon becomes green after approximately one week. However, the tip remains embedded inside the seed, which does not degenerate until well after the emergence of the first leaf(*i.e.* 3–5 weeks after germination). Generally, only 1–3 leaves will form in the first season.

Although there is substantial variation in the rate of embryo development in a given batch of seeds, embryo size is relatively uniform for the first four weeks. By W11, seeds contain embryos ranging in size from an immature embryo of 2.5mm to a germinating embryo of 17mm. After germination, however, growth is extremely rapid accounting for the large size variation noted in Figure 1 after six weeks. During this period, seeds vary from ungerminated to those with emerging seedlings.

Seed development

In *Nerine*, development from pollination to seed maturation, marked by seeds bursting through the ovary wall, can take 3-9 weeks (Table 1). The number of seeds in an individual fruit varies within and between species, ranging from a single seed to 25 seeds per capsule. At maturity, the seeds are large, 3-8mm in length (averages shown in Table 3), fleshy, globose to ovoid, with branched vascular tissue. The single integument consists of a chlorophyllous epidermal layer with stomata, under which is chlorenchymous tissue grading to parenchymous tissue towards the center of the seed. Starch is abundant and evenly distributed through the integument and endosperm.

The size of seeds is variable within and between cultivars of *Nerine* (Table 3). *N. bowdenii* x 'Clone 63' produces seeds ranging from 3-8mm while seeds of *N. flexuosa* 'Alba' and *N. sarniensis* cultivars are smaller, ranging from 3-6mm. Seed size within a single cultivar varies, even when seeds

have originated from the same ovary. However, not all seeds germinate and the likelihood of successful germination generally increases with an increase in seed size. In this study, seeds under 4mm in length (from all seed parents) had a markedly lower germination rate than seeds ≥ 4mm (Table 3). In *N. bowdenii* x 'Clone 63', *N. flexuosa* 'Alba', as well as the *N. sarniensis* cultivars x 'Jill' and x 'Rosea', seeds ≥ 5mm had a significantly higher germination rate than 4-5mm seeds. *N. sarniensis* cultivars x 'Pink Fairy', x 'Sunset Falls' and x 'Xanthia' showed little or no difference in germination rates in seeds from the 4-5mm and ≥ 5mm classes. The *N. sarniensis* cultivars x 'Captain Dunne Cook', x 'Fred Danks' and x 'Brahms' produced smaller seeds with none measuring over 5mm. In the latter two cultivars, the 4–5mm seeds had germination rates of 93% and 100% respectively.

Germination

Seeds can germinate at room temperature with no exogenous water or nutrient supply and in the absence of light. Seeds have been observed germinating on the laboratory bench and in seed envelopes kept on laboratory shelves. In controlled conditions of 20°C and 25°C, no significant differences were found between germination percentages of batches kept in light or dark conditions (data not shown).

The time taken for germination is variable within and between species, taking 2–11 weeks after seed shed (Table 1). *N. bowdenii* was relatively slow to germinate and the timing of fresh seed germination varied considerably (4–11 weeks after seed shed). Faster germination occurred in *N. flexuosa* 'Alba', *N. masonorum*, *N. sarniensis* x 'Jill' and *N. sarniensis* x 'Rosea'. Under identical conditions, germination time in *Nerine* can vary even when seeds are collected on the same day (Fig. 2). Batches of seed from the fast germinating species *N. sarniensis* x 'Rosea' exhibited 100% germination within a six week period, while it took nine weeks for 100% germination in *N. bowdenii* x 'Clone 63' (Fig. 2). The related species, *Amaryllis belladonna*, has a chlorophyllous embryo at seed shed and germination is rapid, occurring within three weeks of seed shed (Fig. 2).

Seeds that disintegrated within the first 3–4 weeks of the germination trial were assumed to be inviable. Embryos were not located in these seeds. Such seeds were commonly found in batches from *N. bowdenii* and *N. flexuosa* 'Alba', occurred rarely in *N. sarniensis* x 'Rosea' and *N. sarniensis* x 'Jill', and were not seen in *N. undulata*. The percentage of inviable seed in any particular seed batch showed no correlation with treatment or age of seed.

Temperature and storage

To determine if temperature affected seed germination, seeds of *N. bowdenii* x 'Clone 63' and *N. sarniensis* x 'Rosea' were incubated at temperatures ranging from 4–30°C (Table 4). Temperatures of 20 and 25°C were optimal for seed germination in both cutivars tested, with germination rates of 100% well inside the trial period of three months. Exposure to 30°C for two weeks was sufficient to cause seed degeneration in *N. bowdenii* x 'Clone 63'.

Temperatures of 10°C and 15°C did not affect actual percentage germination in either *N. bowdenii* x 'Clone 63' or *N. sarniensis* x 'Rosea', but did influence germination rate (Table 4). A temperature of 10°C caused the germination rate in both cultivars to slow down significantly. In *N. sarniensis* x 'Rosea', a period of four months was required for all seeds to germinate. This compares with less than two months under optimal conditions. A temperature of 15°C did not significantly slow germination in this cultivar. These low temperatures had a greater effect on full germination rate of *N. bowdenii* x 'Clone 63'; seven months at 10°C and five months at 15°C (compared to 2–3 months at optimum temperature).

The effect on germination was more marked at 4°C. Seeds of *N. bowdenii* x 'Clone 63', *N. flexuosa* 'Alba', *N. undulata* and *N. sarniensis* x 'Jill' can be stored at 4°C without germination. In *N. sarniensis* x 'Rosea' and *N. masonorum* storage at 4°C will slow the germination rate but some germination will occur (40% after three months and 100% after seven months in *N. sarniensis* x 'Rosea' [Table 4]). This is also the case in the related species *A. belladonna* where 4°C slowed, but did not prevent, germination. In fact, all seeds of *A. belladonna* stored at 4°C germinated within a two month period (Table 5).

Periodical dissection of *N. bowdenii* x 'Clone 63' seeds stored at 4°C storage was performed to investigate embryo status. In all cases, embryo growth was suspended, which in turn prevented sufficient development for germination. Even after 12 months storage, 39% of embryos were ≤0.5mm in length (Table 6). This is comparable to the percentage of this size class found after only four months storage (30%) and suggests embryo size does not increase after entering low temperature storage. Embryo growth in *N. bowdenii* x 'Clone 63' resumes when removed from cold storage and placed in 20°C, whereupon germination will occur as normal.

Storage at 4°C for two months, before transfer to 20°C, did not affect germination percentage in *N. bowdenii* x 'Clone 63' and *N. sarniensis* x

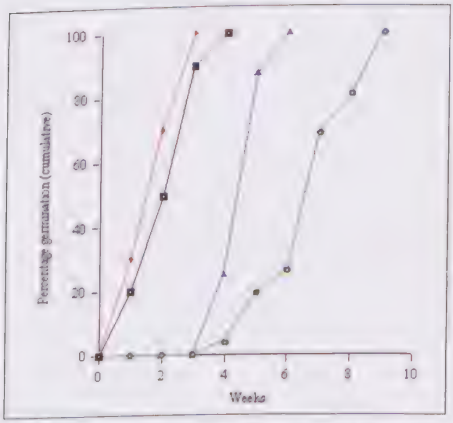

Fig. 2: Germination of open pollinated seeds at room temperature.

Plate 1a. Longitudinal section of *N. masonorum* seed (stained with Calcofluor), showing pro-embryo and suspensor cells at seed shed. Also evident are the multi-layer integument and endosperm . Proembryo length = 60µm.

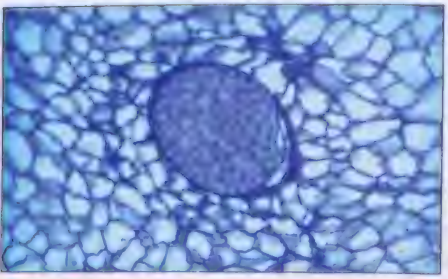

Plate 1b. Longitudinal section of *N. masonorum* seed (stained with Toluidine Blue), showing globose embryo one week after seed shed. Embryo has expanded to fill the width of the embryo sac. Suspensor is still visible. Embryo diameter = 120µm

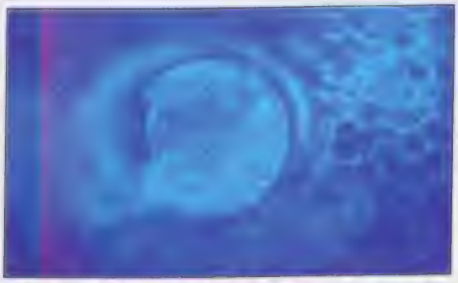

Plate 1c. Developing embryo of *N. bowdenii* x 'Clone 63' (stained with Calcofluor), four weeks after seed shed. The embryo is now polar, curling inwards to form a crescent shape, with a central bulge of dividing cells. A distinct epidermis is visible. Embryo length = 240 µm.

Plate 1d. Longitudinal section of *N. bowdenii* x 'Clone 63' embryo, dissected from seed, six weeks after seed shed. Note elongated procambial cells. Embryo length = 2mm.

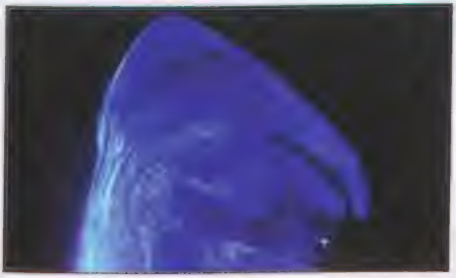

Plate 1e. Longitudinal section of *N. bowdenii* x 'Clone 63' embryo at germination. The cap of protective cells is evident at the tip. Embryonic leaves are seen at the shoot apex positioned behind the tip. Embryo width = 0.7mm.

'Rosea' (Table 5). The germination rate in both *N. sarniensis* x 'Jill' and *N. flexuosa* 'Alba' showed a slight drop after two months of storage, yet remained over 70% (Table 5). Longer periods of storage, without significant effect on germination, were also possible with *N. bowdenii*, *N. flexuosa* 'Alba' and *N. undulata*. In the latter two species, seed successfully germinated following removal from a six month period of cold storage (it should be noted that the sample size of *N. undulata* was very small [1]; Brown, unpublished data). Effect of cold storage on *N. bowdenii* was examined in more detail, with batches of seeds stored for up to nine months (Table 7). A high germination rate persisted, with percentage of viable seed germinating exceeding 80% for the duration of the study. Although the batches showed a variation in number of viable seed, there was no correlation between number of inviable seeds and length of storage (Table 7).

DISCUSSION

Nerine seeds are fleshy and do not undergo a dormancy period. Water-rich seeds are found in several members of the Amaryllidaceae including *Clivia*, *Haemanthus*, *Hymenocallis* Salisb., *Amaryllis*, *Boophane* and *Brunsvigia*. The seeds of the latter three genera are bitegmic, unlike the unitegmic seeds of tribe Amaryllideae, including *Nerine* (Snijman and Linder, 1996). *Crinum* seeds, also fleshy, differ anatomically from *Nerine* in that the outer layers of the endosperm become corky during development (Howell and Prakash, 1990). In *Nerine*, the integument increases after fertilization, in part due to cell division. This also occurs in *Hymenocallis* (Whitehead and Brown, 1940), but in this genus the bulbs of the seeds volume is integumentary tissue rather than endosperm.

At seed shed, the embryo of *Nerine* is at the pro-embryo stage and development proceeds in a period of after-ripening that may take 3-10 weeks. Development of the embryo progresses through a globose stage and a bipolar almond shape before assuming a club shape at maturity. The embryo is linear according to the classification of Martin (1946, cited in Bhatnagar and Johri, 1972), a common characteristic of the Amaryllidaceae (Dahlgren and Clifford, 1982). The necessary period of after-ripening also occurs in *Hymenocallis* and *Crinum* (Whitehead and Brown, 1940; Howell and Prakash, 1982) but not in *Amaryllis* where the embryo is chlorophyllous and mature with recognizable organs at seed shed. According to Whitehead and Brown (1940), the after-ripening condition of seeds is intermediate between true vivipary (seeds where germination occurs while remaining connected

to the parent plant) and seeds with dormancy mechanisms (usually being dehydrated and requiring water to break dormancy). However, there are reports of seeds of *Nerine* (Dyer, 1976), *Crinum* (Howell and Prakash, 1982) and *Hymenocallis* (Newton, 1985) germinating before being shed. Howell and Prakash (1982) suggest that these seeds, with occasional precocious germination, may be an evolutionary precursor to vivipary.

At germination, the widest pole of the mature embryo remains embedded in the seed, while the opposite pole elongates, and emerges from the seed. At this stage the embryo remains rudimentary in external morphology, non-chlorophyllous, and has no leaf or root structures. The lack of differentiation into organs is unusual; normally mature embryos have a recognizable radicle, plumule and cotyledon (Bhatnagar and Johri, 1972). Emergence of the coyledon is followed by formation of a probulb at the distal pole. Subsequent development of the contractile root in turn precedes the appearance of true leaves by 2-3 weeks. This pattern of germination is similar to that reported in *Hymenocallis* (Whitehead and Brown, 1940) and *Crinum* (Pate and Dixon, 1982).

Nerine seeds do not degenerate until true leaves have formed, suggesting they are important as a nutrient source for the small seedling. This is supported by the fact that germination and seedling development can occur in the absence of moisture, light or exogenous nutrients. This phenomenon has also been reported in *Hymenocallis* (Whitehead and Brown, 1940) and *Crinum* (Isaac and McGillivray, 1965). The presence of a stomatose epidermis and sub-epidermal chlorenchymatous tissue suggests that the integument may be a carbohydrate source for the developing embryo/seedling. In *Hymenocallis*, starch is manufactured by the chlorenchymatous tissue of the integument (Whitehead and Brown, 1940). The origin of starch in the integument remains to be determined in *Nerine*, but it may also originate from the chlorenchymatous integumentary tissue.

The action of the contractile root to pull the probulb into the substrate ensures that the bulb will remain covered by soil in future growth phases. This may be a survival adaptation to pull the bulb below the surface for protection prior to the dormant phase, a feature also seen in *Crinum* (Pate and Dixon, 1982). The positioning of the *Nerine* probulb is interesting in regard to numerous reports suggesting that *Nerine* bulbs should be planted with the neck and a substantial part of the bulb out of the ground (Harrison and Harrison, 1967; Yates, 1994). This does not appear to occur in the natural environment.

Temperature appears to be critical in *Nerine* germination with all species sensitive to high temperature. The optimum temperature for germination is approximately 20°C. At 30°C seeds will degenerate, and although germination will occur at 25°C, the germination percentage is reduced. Temperatures of 10°C and 15°C retard germination but do not adversely affect seed viability. *N. sarniensis* x 'Rosea' is less affected by cool temperature than the slower germinating *N. bowdenii* and will germinate even at 4°C, although the germination rate will be slower.

In *N. bowdenii* x 'Clone 63' embryo growth is suspended when stored at 4°C; consequently, germination can be prevented. *N. undulata* and *N. flexuosa* 'Alba' can also be stored at 4°C without germination occurring. Seeds retain their viability and are able to continue development after removal from storage. *Amaryllis belladonna*, however, will germinate at 4°C, with the only effect being a slowing of germination. This phenomenon may be due to the well-developed embryo having passed a commitment point where development cannot be suspended. Consequently, growth and the germination process continue, albeit at a slower rate than in optimum conditions. A similar situation may also exist in *N. sarniensis* x 'Rosea'. As this is a fast germinating species, the after-ripening period is much shorter, and it is possible embryos have developed to a critical stage, prior to arriving in cool storage. Consequently, the germination process continues, although slowed by the cooler temperature. Although a likely scenario, the above is difficult to confirm, as identification of embryo stage requires seed destruction. Similarly, *N. masonorum*, a fast germinating species, will also germinate in cool conditions.

The necessary period of after-ripening and ability to suspend embryo growth in low temperature may be adaptations to environmental conditions. As *Nerine* is an autumn flowering genus, seed set occurs in late autumn/early winter. The suspension or retardation of embryo growth in cold conditions could help seedlings survive adverse winter conditions in the absence of a seed dormancy mechanism. Seeds of *N. bowdenii* x 'Clone 63' can be stored at 4°C for several months and germination will occur once seeds are exposed to warmer temperatures. This suggests that these seeds could survive a cold winter with subsequent embryo growth and germination occurring in warmer spring temperatures. This species is found in montane districts, where winter temperatures are very low. Delaying germination until temperatures rise may also be an advantage where the surface soil is frozen.

As in *N. bowdenii* x 'Clone 63', the seeds of *N. flexuosa* 'Alba' and *N. undulata* showed no decrease in percentage germination after six months in cold storage. Similarly, these seeds may be adapted to survive adverse winter conditions. The seeds of *N. sarniensis* were not as amenable to cold storage as the above species. In *N. sarniensis* x 'Jill', some seeds shrivelled during cold storage. Although germination rate was still quite high (75%), it was markedly lower than that found using fresh seeds (95%). This may be a result of the seeds not being adapted to survive periods of suspended animation due to cold. The natural habitat of *N. sarniensis* would not exhibit the same harsh winters endured by *N. bowdenii*, so seeds may not be capable of suspending growth for long periods. This may also explain why growth cessation does not occur in *N. sarniensis* x 'Rosea' at low temperatures. As both these varieties are hybrids, an alternative possibility is that these observations are due to adaptive properties of the seed being lost in the hybridization process.

The ability to store seeds, without adversely affecting germination, is of horticultural significance. Viability lasts for at least nine months in *N. bowdenii* x 'Clone 63' (Table 7), and for at least six months in *N. flexuosa* 'Alba' and *N. undulata* (Table 5). This would allow use of cool temperatures to slow/suspend germination in these species for later planting or for long-distance seed transportation.

The concept of a minimum size requirement for successful germination of *Nerine* seed is also of significance to plant breeders. Seeds not achieving viable size may be due to: (i) ovules developing without being fertilized (parthenocarpy); (ii) seeds not having sufficiently developed due to late pollination; (iii) arrested development due to lack of maternal resources through competition with other seeds or florets; or (iv) breakdown of the embryo or endosperm as a result of a hybrid cross. In the latter three cases, seeds would have been fertilized and their development may be assisted by artificially supplying nutrients to allow continuation of development. This can be achieved by the culture of small seeds on a nutrient tissue culture medium. Seeds less than 4mm have developed to germination stages on tissue culture media (Brown *et al.* 1998). Consequently, this technique is extremely promising especially for seeds from hybrid crosses. Experiments are currently continuing to determine whether germination rates can be substantially raised by tissue culture. However, one major obstacle is that it is impossible to determine categorically whether an ovule has actually been fertilized.

Embryo rescue is another promising technique available to plant breeders who wish to save failing hybrid crosses. However, the ontogeny of the *Nerine* embryo has significant implications for this technique. Successful embryo rescue usually requires embryos at the post-globular stage. Survival of *in vitro* embryos generally increases with maturity. However, aborting embryos must be excised prior to a breakdown of the endosperm. Therefore, a balance between these two factors must be achieved (Monnier, 1995). In *Nerine*, the post-globular stage can be several weeks after seed shed, in species such as *N. bowdenii*, by which time the endosperm could have already broken down significantly. Isolation and culture of the immature embryo at the time of seed shed requires a specialized culture medium or combination of media for development into a seedling (Brown *et al.*, 1998). Successful embryo rescue has been achieved in embryos less than 1mm dissected from *N. bowdenii* x 'Clone 63', although current success rates are relatively low (Brown *et al.*, 1998). Embryo rescue has been successful in *Hippeastrum* (Bell, 1973) and *Amaryllis belladonna* (Brown, unpublished); however, the embryo in these genera is significantly more developed than the *Nerine* embryo at the stage of isolation. Culture of whole ovules or ovaries is an alternative to excision and culture of the embryo and can be performed very soon after pollination, before any breakdown of endosperm or embryo has occurred. This technique has been successfully employed in *Nerine* (Coertze and Louw, 1990; van Tuyl *et al.*, 1992). A combination of these techniques (ovule culture followed by embryo culture once the embryo has reached an appropriate size for embryo rescue) may be the most appropriate protocol for use in *Nerine*.

See page 160 for Fig. 2.

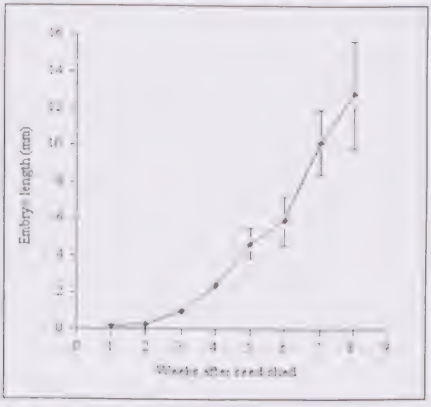

Fig. 1: Mean size (±SE) of *N. bowdenii* x 'Clone 63' embryos.

Table 1. Number of weeks from pollination to seed shed (SS) and seed shed to germination. (G).

Cultivar	SS	G
N. bowdenii x 'Clone 63'	4-8	4-11
N. flexuosa 'Alba'	3-9	4-6
N. masonorum	3-4	3-5
N. sarniensis x 'Jill'	4-9	5-9
N. sarniensis x 'Rosea'	3-9	2-7

Table 2. Timeline of embryo development for *N. Bowdenii* x 'Clone 63'.

Weeks after anthesis	Event	Developmental stage
W0	Anthesis	
W1	Pollination	
W2		Fertilization
W3		Enlargement of seeds
W4		
W5	Seed shed	Pro-embryo
W6		Globose embryo
W7		Polar embryo
W8		Epidermis evident
W9		External differentiation
W10		Rapid elongation (procambium evident)
W11		Embryonic leaves present
W12	Germination	
W13		External bulge at radicle pole
W14		
W15		Contractile root
W16		
W17		Leaf emergence

Table 3. Average seed size and percentage seed germination for 3 size classes. Total number of seeds scored per size class in parentheses.

SEED PARENT	Seed length	% seed germination		
		2.5≤x<4mm	4≤x<5mm	≥5mm
N. bowdenii x 'Clone 63'	5.6±0.1	32 (28)	62 (29)	92 (49)
N. flexuosa 'Alba'	4.8±0.2	0 (35)	28 (36)	60 (40)
N. sarniensis x 'Brahms'	3.6±0.2	0 (15)	100 (2)	-
N. sarniensis x 'Captain Dunne Cook'	3.8±0.2	25 (4)	50 (12)	-
N. sarniensis x 'Fred Dank'	3.9±0.1	14 (7)	93 (14)	-
N. sarniensis x 'Jill'	4.2±0.1	64 (11)	67 (15)	95 (42)
N. sarniensis x 'Pink Fairy'	4.8±0.1	8 (13)	47 (34)	53 (70)
N. sarniensis x 'Rosea'	4.2±0.1	19 (68)	68 (41)	85 (13)
N. sarniensis x 'Sunset Falls'	4.1±0.1	20 (5)	80 (24)	88 (17)
N. sarniensis x 'Xanthia'	4.6±0.2	75 (4)	100 (11)	100 (18)

Table 4. Percentage germination after three months and after seven months (in parentheses), at different temperatures for *N. bowdenii* x 'Clone 63' and *N. sarnienses* x 'Rosea'.

Cultivar	4°C	10°C	15°C	20°C	25°C	30°C
N. bowdenii x 'Clone 63'	0(0)	0 (100)	90 (100)	100 (100)	100 (100)	0 (0)
N. sarniensis x 'Rosea'	40 (100)	80 (100)	90 (100)	100 (100)	100 (100)	n/a

Table 5. Percentage of seeds cold stored for 2 months. Germination trial conducted for 12 months. (*) = seed germination occurred during cold storage. Number of seeds is in parentheses.

Cultivar	No Storage (control)	Cold Storage
N. bowdenii x 'Clone 63'	100 (32)	100 (25)
N. flexuosa 'Alba'	89 (35)	80 (20)
N. sarniensis x 'Jill'	95 (22)	75 (20)
N. sarniensis x 'Rosea'	100 (20)	100 (10)*
N. undulata	100 (6)	100 (4)
Amaryllis belladonna	100 (10)	100 (10)*

Table 6. Percentage of embryos of *N. bowdenii* x 'Clone 63' in three size classes after storage at 4°C (30 seeds scored in each batch).

Storage Period	Percentage of Embryos		
	≤0.5mm	0.5-1.0mm	>1mm
4 months	30	43	27
6 months	30	37	33
8 months	40	30	10
10 months	27	40	33
12 months	39	47	14

Table 7. Germination of *N. bowdenii* x 'Clone 63' seed at 20°C after storage at 4°C. Germination trial conducted for 12 months. Number of seeds scored is in parentheses.

Storage Time	Inviable seed	Viable seed	% Germination (viable seed)
No Storage	2/35	33/35	100
1 week	4/25	21/25	95
2 weeks	0/25	25/25	100
3 weeks	2/25	23/25	86
4 weeks	8/30	22/30	100
2 months	9/25	16/25	100
3 months	3/25	22/25	100
4 months	2/25	23/25	96
5 months	1/20	19/20	83
6 months	1/20	19/20	95
7 months	1/20	19/20	89
8 months	0/20	20/20	85
9 months	5/20	15/20	93

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NOTES ON SOME RARE AND NEWLY PUBLISHED SPECIES OF *LACHENALIA* FROM SOUTH AFRICA AND NAMIBIA

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The distributional range of a number of species belonging to the large genus *Lachenalia* such as *L. mathewsii*, *L. polyphylla*, *L. purpureo-caerulea* and *L. viridiflora* has been greatly reduced due to agricultural and other activities over the past few decades, and has led them to the brink of extinction. However, certain species from southwestern Namibia, as well as the arid northwestern regions of South Africa such as Namaqualand, Bushmanland and the Richtersveld, are considered to be naturally rare, and occupy very narrow distribution ranges. Due to the deciduous nature of the genus, growth and flowering of these arid habitat species is dependent on sufficient seasonal rainfall, and they are adapted to survive long periods of drought. I would like to briefly discuss several such rare species (*L. nordenstamii*, *L. polypodantha* and *L. verticillata*) which were not illustrated in *The Lachenalia Handbook* (Duncan, 1988) due to a lack of living material available at the time, and which are illustrated here in colour for the first time. In addition, two rare new species published in 1997 (*L. inconspicua* and *L. marlothii*) as well as five new species published in 1998 (*L. attenuata*, *L. doleritica*, *L. lactosa*, *L. leipoldtii* and *L. nutans*) are briefly discussed, and with the exception of *L. leipoldtii* and *L. nutans*, illustrated in colour for the first time.

1. *Lachenalia nordenstamii* W.F. Barker

L. nordenstamii is a very rare, dwarf species from the northern Richtersveld, South Africa, and southwestern Namibia. It was first collected in South Africa by Dr B. Nordenstam in 1962, but since then has been collected very infrequently. Its habitat preference is sheltered rock cracks. As with several other *Lachenalia* species from this exceptionally hot, dry area, it is an early-flowering species which takes advantage of good autumn rains (when they do occur) to flower and produce seed by the time extreme heat sets in again in spring. During frequent periods of insufficient rainfall, the bulbs simply remain dormant for one or more growing seasons. The single banded leaf of *L. nordenstamii* is similar to that of *L. buchubergensis* Dinter, another rare species which occurs in the same area. However, the flowers of the latter

species are very distinct, being narrowly cylindrical with slightly exserted stamens, whereas those of *L. nordenstamii* are widely campanulate and have very well-exserted, spreading stamens.

Etymology: the species is named for Dr. B. Nordenstam, well-known Swedish botanist.

Flowering period: late autumn to mid-winter.

Height: 50–120 mm.

Cultivation note: *L. nordenstamii* requires an extremely well drained growing medium and light shade.

2. *Lachenalia polypodantha* Schltr. ex W.F. Barker

L. polypodantha is a very attractive, rare dwarf species from northern Namaqualand and the southern Richtersveld, South Africa. It was collected for the first time by Rudolf Schlechter near Steinkopf in 1896, and has since been collected very infrequently. Its habitat preference is deep sandy flats in full sun, and it usually grows in colonies. Under cultivation, this species often remains completely dormant during the growing season, and in the wild the bulbs are adapted to remain dormant for an indefinite period, until favourable conditions return. *L. polypodantha* is related to *L. angelica* W.F. Barker, another dwarf species which occurs in western Namaqualand. Both species have a single ovate or ovate-lanceolate leaf covered with tiny stellate hairs on the upper surface, and widely campanulate flowers. However, *L. angelica* differs mainly in having a much smaller, prostrate leaf , a much less dense inflorescence, and pure white flowers with white stamens as long as the inner tepals, compared to the raised, spreading leaf and well exserted stamens with purple filaments of *L. polypodantha*.

Etymology: this species' name describes the many foot-shaped anthers.

Flowering period: early to mid spring.

Height: 50–150 mm.

Cultivation note: *L. polypodantha* requires an extremely well drained sandy growing medium anda sunny location.

3. *Lachenalia verticillata* W.F. Barker

L. verticillata is a beautiful, very rare species with a restricted distribution in northern Namaqualand and southwestern Bushmanland. It was collected for the first time by Harry Bolus in 1883, and a second collection was made fifty years later by Paymaster Captain T.M. Salter. Since then, very few collections have been made. The shape of the flowers of this species resembles those of certain forms of *L. elegans* W.F. Barker, which are also urceolate and sessile, but the lower inner tepal of *L. verticillata* is much longer, and the flowers are arranged in distinct, three-flowered verticils. The leaf of *L. verticillata* is distinctly glaucous and deeply channelled, with conspicuous dark brownish purple spots on the lower surface, and is heavily banded on the clasping leaf base. The leaves of most forms of *L. elegans* are dark green, leathery, heavily spotted on the upper surface and not banded on the clasping leaf base. Geographically, the two species are well separated; the widespread *L. elegans* occurs very much further south on the Bokkeveld Plateau, Cederberg and in the western Karoo.

Etymology: *L. verticillata* is named for the arrangement of flowers in three-flowered whorls or verticils.

Flowering period: mid spring.

Height: 100–250 mm.

Cultivation note: *L. verticillata* is easily cultivated in a sunny location.

4. *Lachenalia inconspicua* G.D. Duncan

Lachenalia inconspicua is a rare dwarf species that is only known from a handful of collections made in southern Namaqualand and western Bushmanland. According to current records, the first collection was made as recently as 1982 in western Bushmanland, and it is usually found growing singly in deep red gravelly sand in full sun. As with many other arid habitat *Lachenalia* species, the bulbs often remain completely dormant for one or more growing seasons under cultivation, and the same phenomenon undoubtedly also occurs in the wild. *L. inconspicua* is related to *L. concordiana* Schltr. ex W.F. Barker, another rare dwarf *Lachenalia* with greenish cream flowers which occurs in northern Namaqualand. The latter species also usually has its flowers arranged in three-flowered whorls or verticils. However, itdiffers in having a linear-lanceolate leaf with widely campanulate flowers with dark green markings, and the tips of the inner and outer tepals

FIVE NEWLY PUBLISHED SPECIES

The following new species appeared in **Bothalia** 28(2): 131–139 (1998):

6. *Lachenalia attenuata* W.F. Barker ex G.D. Duncan

Lachenalia attenuata is a poorly collected but fairly widespread species from the Great and Little Karoo, and the southern Cape. It was first collected by Dr. J. Muir in the southern Cape in 1933, and occurs in montane habitats where it is usually encountered growing singly in south-facing, seasonally moist, well-drained loamy clay soil amongst rocks. It is related to *L. hirta* (Thunb.) Thunb. which has similar oblong or oblong-campanulate pale blue flowers with greenish-yellow inner tepals and included or slightly exserted stamens, and a single linear leaf with brownish purple and magenta bands on the clasping leaf base. *L. hirta* var. *hirta* differs mainly in having much longer pedicels, and a leaf that widens abruptly into a loosely clasping base, and with distinct stiff bristles and papillae on the lower surface and margins. There are also differences in seed morphology between the two species, and the distribution ranges do not overlap, *L. hirta* occurring from Namaqualand southwards to the Western Cape.

Etymology: the name describes the gradually tapering leaf.

Flowering period: early to mid spring.

Height: 65–220 mm.

Cultivation note: *L. attenuata* is easily cultivated in a sunny location.

7. *Lachenalia doleritica* G.D. Duncan

Lachenalia doleritica was discovered by Mrs. Margaret Thomas as recently as 1984, and is known from only three collections, all from the Bokkeveld Plateau in the Northern Cape Province. It is a very rare species which appears to be confined to heavy doleritic clay soil where plants occur singly on open flats in full sun. In the wild, the ovate leaves of this species are slightly arcuate and its leaf tips rest at ground level, but under cultivation the leaves are raised above ground. It is related to *L. neilii* W. F. Barker ex G.D. Duncan which has a similar many-flowered inflorescence of greenish oblong-campanulate flowers and usually unmarked leaves, with distinct depressed longitudinal veins on the upper surface. *L. neilii* differs mainly in having smaller flowers with shortly exserted stamens, lanceolate, glaucous, suberect leaves. Its bulb always produces a ring of bulblets at its base. It grows in colonies, and overlaps the narrower range of *L. doleritica*.

exserted, declinate stamens and usually a swollen peduncle and rachis. It differs from *L. leipoldtii* in having a subterranean, very loosely clasping leaf base, a linear, conduplicate, glaucous leaf without markings or thickened leaf margin, and pale magenta inner tepals and filaments.

Etymology: *L. leipoldtii* is named for celebrated South African poet, physician and naturalist Dr C. Louis Leipoldt, who collected this species in 1931.

Flowering period: early to mid spring.

Height: 100–280 mm.

Cultivation note: unknown in cultivation.

10. *Lachenalia nutans* G.D. Duncan

Lachenalia nutans is a rare dwarf species only known from two collections made in the southwestern part of Namibia. It was first collected by M.K. Dinter in 1929, and again by Mrs Nicky van Berkel more than fifty years later, in 1986. Plants grow singly or in groups on sandy gravel flats in full sun. As it occurs in an area which experiences intense heat for much of the year, as well as erratic rainfall, the bulbs are typically deep-seated in order to survive unfavourable conditions, and almost certainly only grow and flower if there has been sufficient seasonal rainfall. *L. nutans* has a dense racemose inflorescence of distinctly nodding, oblong-campanulate, creamy white flowers with declinate, well exserted stamens and a single broadly lanceolate leaf with a dark green upper surface, a glaucous lower surface and a white, deep subterranean clasping leaf base. It is related to *L. anguinea* Sweet, which occurs in deep red sand from the Richtersveld as far south as the Piketberg district, South Africa, and has similar campanulate white flowers with yellowish green or brownish green markings and well exserted white stamens. It differs from *L. nutans* in being an altogether bigger plant with much smaller, spreading flowers produced on very long pedicels, and has a long arcuate, deeply channelled, flaccid, heavily banded leaf.

Etymology: the name describes the distinctly nodding flowers.

Flowering period: late winter to early spring.

Height: 35–110 mm.

Cultivation note: unknown in cultivation.

Fig. 1.

Fig. 2.

Fig. 3.

Clockwise from upper left:

Fig. 1. *Lachenalia nordenstamii* is a very rare dwarf species which grows in sheltered rock cracks.

Fig. 2. *Lachenalia polypodantha* has a single spreading leaf covered with tiny stellate hairs.

Fig. 3. *Lachenalia verticillata* has its flowers arranged in distinct three-flowered verticils or whorls.

Fig. 4. *Lachenalia inconspicua* in habitat. This rare dwarf species occurs in deep, red, gravelly sand.

Fig. 5. *Lachenalia marlothii* has heavily scented flowers and a single leathery leaf.

Fig. 6. *Lachenalia attenuata* favours south-facing montane habitats in loamy clay soil.

Fig. 4.

Fig. 5.

Fig. 6.

Fig. 7. *Lachenalia doleritica* is a rare species confined to doleritic clay soil.

Fig. 8. *Lachenalia lactosa* in habitat. A late-flowering species, always with a heavily blotched peduncle.

All photographs by Graham Duncan.

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THE NEW PHYLOGENY OF THE AMARYLLIDACEAE

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A SHORT INTRODUCTION TO MOLECULAR SYSTEMATICS

The use of molecular data in phylogeny reconstruction of plants has burgeoned in the last 20 years. In fact, one of the most widely publicized "sound bites" from the recent XVI International Botanical Congress, held in St. Louis this year, was that the "true" green plant family tree was finally about to be realized. Most plant taxonomists would probably agree.

Initially, variation of the fine structure of chloroplast DNA (plastid DNA) was found to be very useful in systematic studies (Palmer and Zamir, 1982; Palmer et al., 1983; Clegg et al., 1984; Kung et al., 1982; Kumar et al., 1982; Palmer et al., 1983) using DNA digests with restriction enzymes. At first, restriction fragments in stained agarose gels were merely compared visually to create a presence/absence data matrix (Clegg et al., 1984; Palmer, 1985; Palmer and Zamir, 1982). The approach was later refined by blotting the fragments onto nitrocellulose or nylon membranes and hybridizing with a radioactive probe of cloned plastid DNA to create restriction site maps of the chloroplast genome (e.g., Sytsma and Schaal, 1985; Sytsma and Gottlieb, 1986; Coates and Cullis, 1987; Jansen and Palmer, 1988; Palmer et al. 1988; Zurawski and Clegg, 1988). Informative restriction site mutations are then subjected to phylogenetic (cladistic) analyses (see below). Phylogenetic relationships in Agavaceae (Bogler and Simpson, 1995), Asteraceae (Jansen and Palmer, 1988; Jansen et al., 1990; Miao et al., 1995; Reiseberg et al., 1991; Schilling and Jansen, 1989; Turner and Kim, 1990; Wallace and Jansen, 1990), *Clarkia* Pursh (Sytsma and Gottlieb, 1986), *Coffea* L. (Berthou et al., 1983), *Ipomoea* L. (McDonald and Mabry, 1992), *Lycopersicon* Miller (Palmer and Zamir, 1982), *Nicotiana* L. (Kung et al., 1982), Orchidaceae (Chase and Palmer, 1992), *Persea* Miller (Furnier et al., 1990), *Pisum* L. (Palmer et al., 1985), *Prunus* L. (Kaneko et al., 1986), and Zamiaceae (Caputo et al., 1991), to name a few, have been established using plastid

DNA RFLPs. Olmstead and Palmer (1994) reviewed the history of plastid DNA RFLP studies and the advantages and limitations of this approach. Perhaps the most serious limitation is the fact that plastid DNA is inherited as a single linkage group, thus a phylogeny within which introgression and hybridization has occurred may not be accurately resolved by restriction site mutation analysis (Doyle, 1992). Moreover, divergence within the chloroplast genome may be too large to permit comparisons within families that are either ancient or have experienced very rapid rates of plastid DNA evolution (Olmstead and Palmer, 1994). At the other extreme, closely related species may not exhibit sufficient variation of the relatively conserved chloroplast genome to be phylogentically useful (Schilling and Jansen, 1989; Olmstead et al., 1990; Reiseberg et al., 1991).

With the advent of polymerase chain reaction (PCR) technology (Saiki et al., 1988), direct comparison of the nucleotide sequences of organismal DNA became possible. Sequencing has certain advantages over restriction site analysis of RFLPs. For one, the taxonomic level at which sequence data can be applied is less constrained than restriction site mapping, depending on the gene chosen for sequencing (Olmstead and Palmer, 1994). Only small quantities of DNA are necessary (Edwards et al., 1991), and even partially degraded material (e.g., herbarium specimens) have yielded PCR quality DNA (Golenberg et al., 1990). Sequence data permit direct comparisons of DNA variation, wherein a single base position functions as a character in phylogenetic analyses. In restriction site mapping, a six or four base-pair sequence is used indirectly to infer a phylogenetically informative mutation (i.e., presence or absence of a given restriction site).

Genes appropriate for sequencing must meet several criteria (Olmstead and Palmer, 1994). The sequence must be of sufficient length to provide enough phylogentically informative data. A sequence divergence rate of 5-15% among the taxa studied is considered sufficient distance to minimize homoplasy (independent occurrence of the same nucleotide change at a given position) while providing enough characters for analysis (Ritland and Clegg, 1990). The sequences must be readily alignable for accurate assessment of homology. Finally, sequences must be orthologous, i.e., homologous by phylogeny (the same gene), rather than paralogous, i.e., sequences related by duplication within the genome (Sanderson and Doyle, 1991; Doyle, 1992). Chloroplast genes meet these criteria very well, and have dominated in the sequence literature to date. Approximately 20 genes from the chloroplast genome are currently considered suitable for phylogenetic

studies (Sugiura, 1989; Wolfe, 1991; Olmstead et al., 1993; Olmstead and Palmer 1994). The majority of studies have focused on the gene for the large subunit of ribulose-1,5 buphosphate carboxylase or rubisco (*rbc*L), due to early studies indicating its phylogenetic utility (Ritland and Clegg, 1987; Palmer et al., 1988) and the wide availability of internal sequencing primers from the DNAX Research Institute in Palo Alto, CA. Over 1000 *rbc*L sequences have been recorded for angiosperms (Olmstead and Palmer, 1994). Much of the work with *rbc*L sequences was featured in a series of papers that comprised volume 80 (no. 3) of the Annals of Missouri Botanical Garden of which Duvall et al. (1993), exploring the phylogenetic relationships of the monocotyledons, and Chase et al. (1993), analyzing *rbc*L sequences across all major taxonomic groups of the angiosperms, were the most far-reaching. By and large, the utility of *rbc*L is restricted to the family level and higher ranks due to the highly conserved nature of the coding region. In the palms, insufficient variation has created difficulty in phylogenetic studies (Hahn et al., 1995; Wilson et al., 1990).

Less conserved coding or non-coding plastid DNA, such as the *rps*16 intron (e.g., Fumariaceae: Liden et al., 1997; Caryophyllaceae tribe Sileneae: Oxelman et al., 1997); *atp*B-*rbc*L spacer (Rubiaceae tribe Rubieae: Manen and Natali, 1995; *Nothofagus*: Setoguchi et al, 1997; ferns: Wolf, 1997), *mat*K (e.g., Higher hamamelids: Manos and Stelle, 1997), *ndh*F (Acanthaceae: Scotland et al, 1995; Bromeliaceae: Terry et al., 1997) or the *trn*L intron/*trn*L-F spacer region, can sometimes yield a higher level of resolution in phylogenetic analyses and/or be applied to questions of lower taxonomic rank. The *trn*L-F region of plastid DNA, for which Taberlet et al. (1991) had developed "universal" primers for amplification, has been used in phylogenetic studies of *Coffea* (Cros et al., 1998). Crassulaceae (Kim et al., 1996; Mes et al., 1996, 1997), Gentianeae (Gielly and Taberlett, 1996; Gielly et al., 1996), Paeoniaceae (Sang et al., 1997), Proteaceae (Maguire et al., 1997), Ranunculaceae (Kita et al., 1995), Amaryllidaceae (Meerow et al., 1999) among others, either alone or in combination with other loci. This region of the plastid genome evolves more than three times than *rbc*L (Gielly and Taberlet, 1994), and can therefore potentially add increased resolution to a phylogeny generated by *rbc*L sequences.

The nuclear genome of plants has been used much less often for sequence-based phylogenetic studies (Hillis and Dixon, 1991). Portions of the small (18S) and large (26S) subunits of genes coding ribosomal RNAs have been sequenced extensively by Zimmer and colleagues (Arnold et al., 1990; Bult et

al., 1995; Hamby and Zimmer, 1988, 1992; Zimmer et al., 1989; Knaak et al., 1990). The 18S and 26S subunits of nrDNA are separated by two internal transcribed spacer regions, ITS1 and ITS2, and a 5.8S gene located between the two ITS regions (Fig. 1). ITS1 varies in angiosperms from 187-298 bp, and ITS2 from 187-252 bp (Baldwin et al., 1995). Though part of the transcriptional unit of nrDNA, the ITS RNA segments are not incorporated into the ribosomes, but are thought to function in the maturation of the rRNAs (Musters et al, 1990; van Nues et al., 1994; van der Sande et al., 1992).

The two ITS regions of 18S-26S nrDNA evolve more rapidly than the coding regions they separate. For closely related taxa, rapidly evolving, non-coding regions of nuclear genes such as ITS can potentially yield a greater degree of informative sequence variation than the more highly conserved coding regions. From a practical standpoint, the small size of the ITS region, and its location between highly conserved sequences, make the spacers easy to amplify by PCR (Baldwin et al. 1995).

Phylogenetic analysis

Phylogenetic analysis (cladistics) has become the standard methodology for testing hypotheses of phylogeny among organisms in systematic biology (Wiley, 1981) based upon principles formally enumerated by Hennig (1966). The main principle of cladistics defines any inclusive group of organisms (a clade), regardless of taxonomic rank, by the presence of one or more shared, derived character states (apomorphies). Such a group is described as being monophyletic. To accept a taxonomic grouping based on shared primitive character states (plesiomorphies) is not acceptable, and results in polyphyletic (taxonomic groups with multiple evolutionary origins) or paraphyletic groups (groups from which one or more members of common descent are excluded). The further principle of parsimony, the most widely utilized approach in cladistics, states that the shortest possible phylogenetic tree (or cladogram), that is the one that requires the least number of steps (character state changes), is the most accurate. The computer programs used by biologists for cladistic analysis attempt to find the shortest possible (i.e., the most parsimonious) phylogenetic tree produced by a particular character state matrix. Typically, the larger the number of informative (versus neutral or ambiguous) characters in the matrix, the smaller the number of equally parsimonious trees. In the most versatile programs used for this purpose, the researcher can apply various weighting schemes or other assumptions about character evolution to some or all of the data. Several confidence tests of a

particular phylogenetic resolution are employed by systematists, the most widely used being the bootstrap analysis (Felsenstein, 1985, 1988; Hillis and Bull, 1993; Sanderson, 1989). A high bootstrap value for a particular clade is a sign of robustness; a low value means that the clade is not well-supported. Does cladistics work? Simulations with known lineages of organisms have shown that parsimony algorithms do a very accurate job of capturing the true phylogeny of a group.

PHYLOGENY OF THE AMARYLLIDACEAE

Amaryllidaceae J. St.-Hil., a cosmopolitan (predominantly pantropical) family of petaloid monocots, represent one of the elements of the Linnaean *Hexandria monogynia* (Linnaeus, 1753), the 51 genera of which have been variously classified since as liliaceous or amaryllidaceous. This basic dichotomy represents the generally uncertain placement of many petaloid monocots until the past two decades. Seven of the 51 genera that Linneaus placed in *Hexandria monogynia* have since been included within a common taxonomic unit, as order Amaryllidaceae (Lindley, 1836; Herbert, 1837), suborder Amarylleae (Baker, 1888), family Amaryllideae (Jaume St. Hilaire, 1805; Brown 1810; Hutchinson, 1934, 1959), subfamily Amaryllidoideae (Pax, 1888; Traub 1963), tribe Amarylleae (Bentham and Hooker, 1883), and section Narcissi (Adanson, 1763; de Jussieu, 1789). Brown (1810) was the first to propose that the genera with superior ovaries be excluded from Amaryllidaceae, a restriction followed faithfully until Hutchinson (1934). Herbert (1837) recognized that Taccaceae was not allied to Amaryllidaceae, and Pax (1888) formally removed Velloziaceae as part of the family (Herbert's suborder Xerophyteae). Hutchinson's (1934, 1959) classification was the first radical recircumscription of Amaryllidaceae since Brown (1810). In defining unifying character of the family to be '... an umbellate inflorescence subtended by an involucre of one or more spathaceous bracts,' he segregated Agavaceae, Hypoxidaceae and Alstroemeriaceae, and added tribes Agapantheae, Allieae and Gilliesieae (Alliaceae). Takhtajan (1969) recognized Amaryllidaceae in the narrowest sense, and maintained a distinct Alliaceae. Cronquist (1988) and Thorne (1976) included Amaryllidaceae within broad concepts of Liliaceae.

Concepts of familial and ordinal limits of the monocotyledons were radically challenged by Huber (1969), who emphasized less conspicuous characters, particularly embryological characters, over gross floral or vegetative morphology. Huber's work highlighted the heterogeneity present in many

traditional monocot families, especially Liliaceae. Much of this work was refined and placed into phylogenetic context by Dahlgren and coworkers (Dahlgren and Clifford, 1982; Dahlgren and Rasmussen, 1983; Dahlgren, Clifford, and Yeo, 1985). In Dahlgren, Clifford, and Yeo's (1985) synthesis, Amaryllidaceae and Alliaceae are both recognized as members of the order Asparagales, an order of 31 families that have evolved many traits in parallel with Liliales. One of the most important and consistent characters separating these two orders is the presence of phytomelan in the seed coat of Asparagales (Huber, 1969). To date, phylogenetic analyses of the monocotyledons, based on both morphological and gene sequence matrices, have supported this classification with some amendment (Duvall et al., 1993; Stevenson and Loconte, 1995; Chase et al., 1995a, b), but the precise relationship of Amaryllidaceae to other Asparagales remained elusive until Fay and Chase (1996) used molecular data to argue that Amaryllidaceae, Agapanthaceae, and Alliaceae form a monophyletic group and that together they are related most closely to Hyacinthaceae s.s. and the resurrected family Themidaceae (the former tribe Brodiaeeae of Alliaceae).

Despite a lack of consensus on generic limits and tribal delimitations within the Amaryllidaceae, cladistic analysis has only rarely been applied to problems in the family, such as by Nordal and Duncan (1984) for *Haemanthus* and *Scadoxus*, two closely related, baccate-fruited African genera, Meerow (1987a, 1989) for *Eucrosia* and *Eucharis* and *Caliphruria*, respectively, and Snijman (1994) and Snijman and Linder (1996) for various taxa of tribe Amaryllideae, and Meerow et al. (1999) for multiple plastid sequences across the entire family. Applying phylogenetic studies for the entire family is difficult due to homoplasy for many conspicuous characters within this highly canalized group (Meerow, 1987a, 1989, 1995). Applying phylogenetic studies for the entire family is difficult due to homoplasy for many conspicuous characters within this highly canalized group (Meerow, 1987a, 1989, 1995). This led Meerow (1995), in a review of evolutionary trends within the family, to conclude that "future reconstruction attempts will greatly benefit from the inclusion of molecular data."

The four most recent infrafamilial classifications of Amaryllidaceae are those of Traub (1957, 1963), Dahlgren et al. (1985), Müller-Doblies and Müller-Doblies (1996) and Meerow and Snijman (1998). Traub's scheme included Alliaceae, Hemerocallidaceae and Ixioliriaceae as subfamilies, following Hutchinson (1934, 1959) in part. Within his subfamily Amarylloideae, he erected two informal taxa, "infrafamilies" Amarylloidinae

and Pancratioidinae, both of which were polyphyletic (Meerow, 1995). Dahlgren et al. (1985) dispensed with any subfamilial classification above the level of tribe, recognizing eight, and treated as Amaryllidaceae only those genera in Traub's Amarylloideae. Stenomesseae and Eustephieae were combined. Meerow (1995) resurrected Eustephieae from Stenomesseae and suggested that two new tribes might need to be recognized, Calostemmateae and Hymenocallideae. Müller-Doblies and Müller-Doblies (1996) recognized ten tribes (among them Calostemmateae) and nineteen subtribes, many of them monogeneric; Meerow and Snijman (1998) recognized 13 tribes, with two subtribes only in one of them. A discussion of character evolution within the family can be found in Meerow (1995) and Meerow et al. (1999).

MOLECULAR SYSTEMATICS OF THE AMARYLLIDACEAE

Insights from plastid DNA sequences *rbc*L and *trn*L-F

Fay and Chase (1996), on the basis of a phylogenetic analysis of *rbc*L sequence data, recircumscribed Amaryllidaceae to include *Agapanthus*, previously included in Alliaceae, as subfamily Agapanthoideae, and resurrected the family Themidaceae for the western North American and Mexican genera of Alliaceae (tribe Brodiaeeae). All the epigynous genera (Amaryllidaceae *sensu stricto*) were treated as Amaryllidaceae subfamily Amaryllidoideae. Bootstrap support for the sister relationship of Agapanthus and Amaryllidaceae was weak (63%). Moreover, the sampling within Amaryllidaceae s.s. (only 4 genera) in Fay and Chase (1996) did not allow sufficient resolution of the generic relationships within the family.

Meerow et al. (1999) presented cladistic analyses of plastid DNA sequences *rbc*L and *trn*L-F alone and in combination for 51 genera of Amaryllidaceae and 31 genera of related asparagalean families. Topologies of the respective plastid sequences were highly congruent and thus were combined. The combined analysis was the most highly resolved of the three (Fig. 1) and provided good support for the monophylly of Amaryllidaceae and indicated Agapanthaceae as its sister family (though bootstrap support for this relationship was still weak at 60%). Alliaceae were in turn sister to the Amaryllidaceae/Agapathaceae clade. Based on these data, it would be possible to argue for recognizing Amaryllidaceae in a modified Hutchinsonian (1934) sense, i.e., with three subfamilies, Allioideae, Agapanthoideae, Amarylloideae. Meerow et al. (1999) opted to recognize a monotypic Agapanthaceae.

Based on the cladistic relationships, the family originated in western Gondwanaland (Africa), and infra-familial relationships are resolved along biogeographic lines. Tribe Amaryllideae, entirely southern African with the exception of pantropical *Crinum*, was sister to the rest of Amaryllidaceae with very high bootstrap support. The remaining two African tribes of the family, Haemantheae (including Gethyllideae) and Cyrtantheae, were well supported, but their position relative to the Australasian Calostemmateae and a large clade comprising the Eurasian and American genera, was not clear. Most surprising, the Eurasian and American elements of the family were each monophyletic sister clades. Internal resolution of the Eurasian

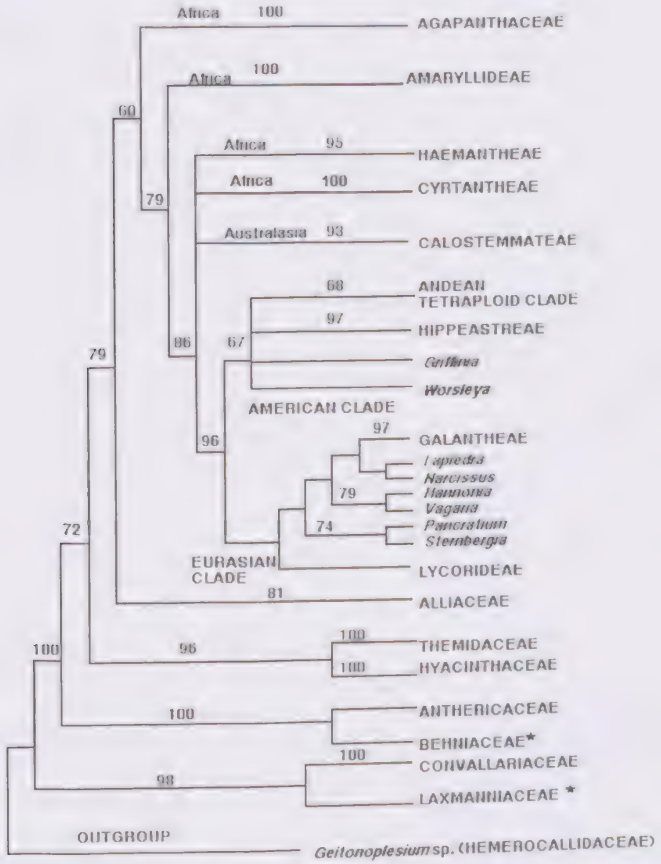

Fig. 1. Strict consensus of 5000 equally parsimonious trees generated by cladistic analysis of successively weighted combined *rbc*L and *trn*L-F sequence matrix for Amaryllidaceae and other Asparagalean genera. Numbers above branches are bootstrap support percentages. Geographic position of major clades is indicated. An asterisk after a terminal taxon indicates that a single species was used as an exemplar in the analysis.

clade only partially supported currently accepted tribal concepts and few conclusions could be drawn on the relationships of the genera based on these data. A monophyletic Lycorideae (Central and East Asian) were weakly supported. *Galanthus* and *Leucojum* (Galantheae pro parte) were supported as sister genera by the bootstrap. The American clade showed a higher degree of internal resolution. Hippeastreae (minus the unresolved *Griffinia* and *Worsleya*) were well supported, and a distinct subtribe Zephyranthinae was resolved as well. A distinct Andean clade marked by a chromosome number of $2n = 46$ (and derivatives thereof) was resolved with weak support. Within the Andean group, a petiolate subclade resolved in the *rbc*L phylogenies, but not in the trnL-F or combined analysis. Five recognized tribes of Amaryllidaceae are consistently resolved by the plastid DNA sequences, and all receive strong bootstrap support (Fig. 1). These are the Amaryllideae, Haemantheae, Calostemmateae, Galantheae and Hippeastreae. Lycorideae is also resolved, but without support.

Ito et al. (1999) resolved a very similar topology for a more limited sampling of Amaryllidaceae and related asparagoids using plastid *mat*K sequences, but *Agapanthus* was sister to a diverse clade of Agavaceae, Anthericaceae, Funkiaceae and Hyacinthaceae in their trees, the former three families represented by a single species each. There was no bootstrap support for this position of *Agapanthus* in their analyses.

Results from nuclear ribosomal DNA ITS sequences. ITS sequences for 76 species of American Amaryllidaceae were used in our most recent analyses. The tree topologies of our latest matrix using *Pancratium* as outgroup (from the Eurasian sister group to the American clade in plastid DNA analyses; Meerow et al., 1999) gives a highly resolved phylogeny with relatively few unresolved branches (Fig. 2). The American genera of the family form two major subclades. The first, or "Hippeastroid" clade, could be described as the diploid ($n = 11$), primarily extra-Andean element of the family (though several of the genera do have Andean representatives), comprising the genera treated as the tribe Hippeastreae in most recent classifications (Dahlgren et al. 1985, Müller-Doblies and Müller-Doblies 1996; Meerow and Snijman 1998). The second subclade constitutes the tetraploid-derived ($n = 23$), Andean-centered tribes. Moreover, the Andean subclade is characterized by 3 consistent deletions, two in the ITS1 and one in the ITS2 regions.

Hippeastroid clade. Within the Hippeastroid clade, recognition of a distinct tribe Griffineae appears well justified (Fig. 2) with strong bootstrap support (95%). The Chilean genus *Phycella* resolves as sister to the rest of

tribe Hippeastreae. *Hippeastrum* is inarguably monophyletic with the exception of a single species (*H. blumenavium*). *Hippeastrum blumenavium* is an unusual species morphologically (petiolate leaves; few, round turgid seed) which has at times been treated as a species of *Griffinia* (Traub and Moldenke, 1949). ITS sequences suggest that it is much more closely related to *Rhodophiala* then *Hippeastrum*. *Rhodophiala* itself does not resolve as monophyletic. Two species form the first clade to branch after *Phycella*. The remaining *Rhodophiala* species so far included form a monophyletic group with *Hippeastrum blumenavium*, which is in turn sister to one group of West Indian and South American *Zephyranthes*. This clade also has strong bootstrap support (97%).

The tribe Zephyrantheae (Traub, 1963) or Hippeastreae subtribe Zephyranthinae (Müller-Doblies and Müller-Doblies, 1996) are clearly polyphyletic. Meerow (1995) suggested that *Zephyranthes* may represent convergence of two distinct (albeit related) lineages in North (Meso) America and South America, respectively. Our wider sampling of this genus

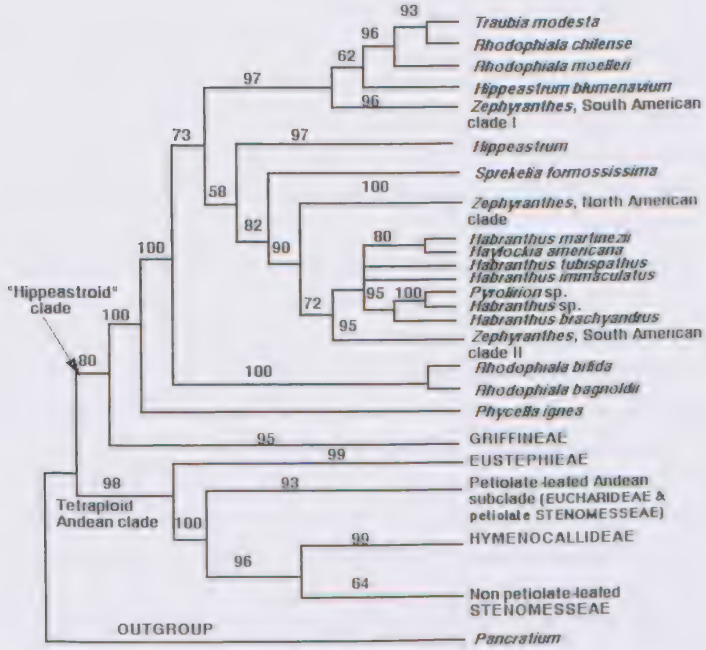

Fig. 2. Strict consensus of 2699 equally most parsimonious trees generated by cladistic analysis of successively weighted nuclear ribsomal DNA ITS sequence matrix with binary gap matrix included for American Amaryllidaceae. Numbers above branches are bootstrap support percentages.

now suggests a putative triple origin for this genus! The rest of Zephyranthineae resolves with moderate support (bootstrap = 82%) as a clade within which *Sprekelia* is basal to a paraphyletic *Habranthus*, and the Mexican/North American species of *Zephyranthes* (Fig. 2).

Andean clade. The Eustephieae are well resolved (bootstrap = 99%, Fig. 2) as a tribe distinct from Stenomesseae as argued by Meerow (1995). Hymenocallideae are also well-supported as a tribe distinct from Eucharideae (bootstrap = 99%), and also sister to the lorate-leafed Stenomesseae. Support for this tribe is confirmed by *rbc*L sequence data (Meerow et. al., 1999). Most surprising is the resolution of a petiolate-leafed clade containing elements of both Eucharideae and Stenomesseae (bootstrap = 93%). While Meerow (1987a) pointed out the probable paraphyly of *Stenomesson*, suggesting that the petiolate-leafed species of that genus might be ancestral to *Rauhia*, *Phaedranassa* and *Eucrosia* (and the extinct *Mathieua galanthoides*), ITS sequences clearly suggest that *Stenomesson* is polyphyletic, and that petiolate leaves evolved only once in the Andean Amaryllidaceae. The lorate-leafed remnants of the Stenomesseae (including *Pamianthe* and *Paramongaia*) form a weakly supported clade, but after the branching of *Pamianthe*, the remainder of the group is robustly supported.

In both of the American subclades, there is a small tribe that is sister to the rest of the subclade, the Eustephieae in the Andean group, and the Griffineae in the Hippeastroid clade. These two small tribes may represent either ancestral or merely very isolated elements of their respective clades.

In a survey of internal morphology of American and African Amaryllidaceae, Arroyo and Cutler (1984) noted several characters that separated American genera from African. All American species surveyed have scapes with collenchyma, a one-layered rhizodermis, and obvolute bracts. All Amaryllideae (entirely African with the exception of pantropical *Crinum*) have schlerenchyma in the scape, a multi-layered rhizodermis, and equitant bracts. *Haemanthus* and *Cyrtanthus* exhibit scape and root anatomy of the American species, but the equitant bracts of Amaryllideae (Arroyo and Cutler, 1984). Calostemmateae (*Calostemma* and *Proiphys*), which were not discussed by Arroyo and Cutler (1984), have equitant bracts. Many of the Eurasian genera have fused spathe bracts which obscures the pattern of their coherence, but both *Lycoris* and *Pancratium* species with free bracts show the equitant condition. *Worsleya* is the only American genus with the equitant bract condition of the Old World genera.

The Amaryllidaceae is one of the larger families of the higher Asparagales. A resolute phylogeny of Amaryllidaceae represents an important contribution to a broader understanding of monocot evolution in general. As the family is highly valued in horticulture, there is more than passing interest among non-scientists in understanding the phylogenetic relationships of the genera. Molecular data has contributed a great deal of resolution towards this goal, and indicates that some changes will be be necessary to the most recent classification of the family (Meerow and Snijman, 1998).

The tribes of the Amaryllidaceae (sensu Meerow and Snijman, 1998, but grouped within larger clades supported by plastid DNA sequence phylogenies (Meerow et al., 1999) and with proposed amendments indicated; base numbers are from Bose and Flory, 1963; Di Fulvio, 1973; Fernandes, 1968; Flory, 1967, 1976, 1977; Flory and Schmidhauser, 1957; Goldblatt, 1976; Inariyama, 1931, 1933, 1937, 1953; Jones and Smith, 1967; Kurita, 1986, 1987a, 1987b, 1987c, 1989; Lakshmi, 1978; Meerow, 1984, 1987a, 1987b; Naranjo and Andrada, 1975; Raina, 1978; Sato, 1938; Traub, 1963; Vosa, 1986; Williams, 1981; Wilsenach, 1965).

Amaryllideae (13 genera, x = 10, 11). The tribe Amaryllideae, marked by its cartilaginous leaf fibers, sclerenchymatous scapes, unique bisulculate pollen with spinulose exines, unitegmic ovules, and bulbiform seeds, is the most robust monophyletic group in the entire family. The relationships among the 13 genera within this tribe have been recently analyzed by Snijman and Linder (1996). In their strict consensus tree of the tribe with Haemantheae as outgroup, two main monophyletic groups are resolved. The first comprises *Crinum*, *Cybistetes* Milne-Rehh. and Schweick, *Ammocharis* Herb., and *Boophane* Herb. (subtribe Crininae), marked in part by a dry, corky non-phytomelanous seed coat. The second clade (subtribe Amaryllidinae) comprises *Amaryllis* L., *Nerine* Herb., *Brunsvigia* Heist., *Crossyne* Salib., *Kamiesbergia* Snijman, *Hessea* Herb., *Carpolyza* Salisb. and *Strumaria* Jacq. Plastid DNA sequence phylogeny for Amaryllidaceae supports the monophyly of this tribe (Meerow et al., 1999) and positions it as sister to the rest of the family, but limited sampling does not explicitly resolve the relationships hypothesized by Snijman and Linder (1996).

Basally Unresolved African and Australasian clades (plastid DNA)

Cyrtantheae (1 genus, x = 8). Consisting of a single African endemic genus, *Cyrtanthus*, this tribe is the only African taxon with the flat, winged phytomelanous seed characteristic of many American genera. It is also the most diverse in floral morphology of any genus in the family.

Haemantheae (4 genera, x = 8, 9, 11, 12). This African tribe comprises the one-seeded berry-fruited genera *Scadoxus*, *Haemanthus*, *Clivia* Lindl., and *Cryptostephanus*. Björnstad and Friis (1972) considered this tribe the most primitive in the family, though the baccate fruit cannot be considered plesiomorphic. Lack of a true bulb occurs in three genera of this tribe (*Clivia*, *Cryptostephanus* and *Scadoxus*, the latter polymorphic). It is has been assumed that this is a plesiomorphic state (Nordal and Duncan, 1984). It is the state that occurs in *Agapanthus*, which in the plastid sequence phylogeny resolution as sister to the whole family. *Cryptostephanus*, while possessing a baccate fruit and a turgid seed, has a phytomelanous seed coat (Meerow, unpubl. data). *Clivia* is the only genus in the tribe with $2n = 22$ chromosomes, while the closely related *Cryptostephanus* has $2n = 24$ (Gouws, 1949).

Gethyllideae (2 genera, x = 6). This tribe consists of two closely related South African endemic genera, *Apodolirion* and *Gethyllis*. Both genera maintain their scapes inside the bulb and have long, fragrant baccate fruits that are multi-seeded. Plastid sequence phylogenies support the monophyly of the tribe but it is firmly nested within Haemantheae, thus recognition as a distinct tribe renders the former paraphyletic (Meerow et al., 1999).

Calostemmateae (2 genera, x = 10). Proiphys and *Calostemma* [$2n = 20$ (Zaman and Chakraborty, 1974)] are an isolated Australasian component of the family. The unique "pseudoseed" of these two genera is actually an adventitious bulbil (Rendle, 1901).

The Eurasian clade

Of the two sister clades, American and Eurasian, supported by plastid DNA (Meerow et al., 1999), the Eurasian clade has so far remained much less resolved. We have encountered difficulty in obtaining clean ITS sequences for many of the genera in this clade.

Lycorideae (2 genera, x = 11). This is the eastern and central Asian lineage of the family. The scape is solid in both genera. The seeds of *Ungernia* are flat and winged; those of *Lycoris* are round and turgid. Blue pigmentation occurs in the flowers of some species of *Lycoris* (Traub and Moldenke, 1949). Plastid sequences place resolve the tribe within a clade of Western European (Meditteranean) genera (Narcisseae, Galantheae, Pancratieae).

Pancratieae (2 genera x = 11). This Old World tribe has uncertain limits and a controversial phylogenetic position. *Pancratium* is the largest genus and the most widespread, from South Africa to the Mediterranean and into

Asia, and the only genus with stamens connate into a staminal cup. The flowers bear a remarkable resemblance to those of *Hymenocallis*. Müller-Doblies and Müller-Doblies (1978) moved *Lapeidra* Lag. and *Hannonia* Braun-Blanq. and Maire from Galantheae to this tribe on the basis of seed and internal bulb morphology (a move not supported by *rbc*L sequence phylogeny). The rudiments of staminal connation are visible in *Lapeidra*. Seeds of the tribe are dry type and phytomelanous, but vary from almost flattened and D-shaped, to turgid and round or wedge-shaped.

Narcisseae (2 genera, x = 7, 10, 11). Together with the closely related Galantheae, this tribe represents the southwest Laurasian element of the Amaryllidaceae. At least some species exhibit $2n = 22$, but much chromosome evolution has occurred in the largest genus *Narcissus* (summarized in Fernandes, 1968). The scape is solid and the spathe bracts are fused into a tube. Seeds are black, dry, round or angular. A "paraperigone" is characteristic of the tribe but absent from *Sternbergia* Walst. and Kit. No relationships with any other tribe outside of Galantheae have been proposed.

Galantheae (5 genera, x = 7, 8, 9, 11, 12). Of similar distribution to that of Narcisseae, the Galantheae are distinguished from the former by anthers dehiscing by apical pores in two genera (*Galanthus* and *Leucojum*), and, according to Artyushenko (1989), the absence of a palisade layer in the leaf mesophyll. Müller-Doblies and Müller-Doblies (1996) treated this tribe as a subtribe of Narcisseae.

The American Clade

Hippeastreae (ca. 10 genera, x = 6, 8, 9, 10, 11, 12?). This is one of the more problematic tribes of neotropical Amaryllidaceae. A hollow scape and some degree of "paraperigonal" development is characteristic. Ravenna (1974) considered *Griffinia* a link between Hippeastreae and Amaryllideae and placed it in its own tribe, Griffinieae. He suggested some relationship to *Worsleya*. Blue range floral pigmentation occurs only in this tribe (the Brazilian endemics *Griffinia* and the monotypic *Worsleya* Traub) and *Lycoris* (Lycorideae), but is common in both *Agapanthus*, Alliaceae, Hyacinthaceae, and Themidaceae. *Griffinia* and *Worsleya* are unresolved in plastid phylogenies, but form a sister clade to the rest of Hippeastreae in the ITS phylogeny (Fig. 2; Meerow et al., 2000a, b). Bootstrap support for the sister group status of Griffineae to Hippeastreae is only moderate, however (80%, Fig. 2), and in trees one step longer than the shortest trees, the Griffineae is unresolved with either the hippeastroid or Andean clade. Together these Brazilian endemics

would appear to represent a relictual Brazilian shield element of the family's early diversification in the neotropics. In fact, this segregate tribe may represent the most ancient elements of the family in the Americas. The fact that *Worsleya* has the equitant bract morphology of the Old World genera lends creedence to this hypothesis (the bracts are fused on one side in *Griffinia*, thus obscuring the pattern of their coherence).

Eucharideae (4 genera, x = 23). This tribe as recognized by Dahlgren et al. (1985) and Traub (1963) is polyphyletic Meerow (1989, 1995). The fleshy, non-phytomelanous (except phytomelanous in *Leptochiton* Sealy) seeds of *Hymenocallis* Salib., *Ismene* Salisb. ex Herb. and *Leptochiton* (tribe Hymenocallideae) and those of *Proiphys* Herb. and *Calostemma* R. Br. (tribe Calostemmateae) are not homologous structures (Rendle, 1901). Furthermore, the phytomelanous seeds of *Eucharis*, *Caliphruria*, *Urceolina* Reichb. and *Plagiolirion* Bak. cannot really be called fleshy and have more structural similarity to the dry types common elsewhere in the family (Meerow, 1989). Not surprisingly, then, both plastid and nrDNA sequences (Meerow et al., 2000a, b) strongly indicate that this tribe is most closely related to the petiolate, flat-seeded genera of Stenomesseae.

Stenomesseae (8 genera, x = 23). This Andean tribe, like the neotropical Eucharideae, is characterized by $2n = 46$ and a well-developed false corona or staminal cup in most of the genera. The seeds are uniformly dry, flattened and obliquely winged. The tribe is polyphyletic according to DNA sequence phylogenies, as is the genus *Stenomesson* Herb. A new tribe, Clinantheae, has been proposed for the linear/lorate-leafed members of this group (Meerow et al., 2000b).

Hymenocallideae (3 genera, x = 23). This tribe consists of three genera, *Leptochiton*, *Ismene* and *Hymenocallis*. The former two are strictly central Andean; Hymenocallis is poorly represented in South America, and primarily North American (SE U.S. and Mexico) and West Indian. The fleshy seeds of Hymenocallideae are comprised of the thick, chlorenchymous outer integument with a well-developed vascular system and a starch-storing embryo (Whitehead and Brown 1940). Phytomelan is absent except in *Leptochiton*.

Eustephieae (3 genera, x = 23). This small tribe represents a southern central Andean clade. The genera (*Eustephia* Cav., *Hieronymiella* Pax and *Chlidanthus* Herb.) have leaves with well-developed palisade layers, exhibit a reduction series in staminal connation, and have trifid stigmas. The seeds are dry, flattened and discoid. The species exhibit aneuploid changes in

chromosome number from the ancestral $2n = 46$ (Di Fulvio, 1973). Ribosomal DNA resolves this tribe as sister to all of the other clades within the Andean group, though only 2 of the three deletions that mark the Andean clade occur in this tribe.

We are continuing of studies of the phylogenetic relationships within and among the tribes of Amaryllidaceae using a variety of DNA sequence data, alone and in combination with a morphological data set (Meerow et al., 2000a). We are optimistic that a stable and accurate phylogeny of the family that will stand the test of time will result from these investigations.

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AN OVERVIEW OF *IN VITRO* PROPAGATION TECHNIQUES APPLIED TO AMARYLLIDS

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INTRODUCTION

The family Amaryllidaceae contains many elegant bulbous plants offerring the horticultural industry almost limitless possibilities of hybrid cultivars. Amaryllids are primarily tropical and subtropical plants, many of which have a long-standing role in horticulture. For the most part, these plants have been introduced into horticulture via numerous European botanists, explorers and settlers of the New World and Africa. *Amaryllis belladona* L. (1753), the type genus of the family, had been introduced into cultivation prior to 1553 (see Seba, plate 17, 1553). In her illustration, Seba included another spectacular amaryllid, *Lycoris radiata* (L'Herit) Herb. Many genera offer highly desirable species and cultivars to horticulture.

A major setback to amaryllid production is the limited supply of desirable parental stock plants. Typically, amaryllid cultivars are propagated by separation of daughter bulbs. This method produces true-to-type clonal cultivars. The process is slow, typically resulting in production of few offsets per season. Many species and hybrdis of the genus *Hippeastrum* Herb. are reluctant to offset (O'Rourke et al., 1991) and, in addition, may prove to be quite difficult to maintain outside their native habitats. Virus-diseased (e.g. *Hippeastrum* mosaic virus) and fungal-contaminated (e.g. *Stagnospora*) bulbs present other problems to the cultivation of amaryllids. If the mother bulb is contaminated, more than likely so will the daughter bulbs, as is commonly the case with many commercially cultivated amaryllids. In this paper I briefly review and evaluate results of the different in vitro techniques applied to members of the Amaryllidaceae.

GENERAL AMARYLLID BULB MORPHOLOGY

True bulbs are complex modified storage organs. With the exceptions of *Clivia* Lindl., *Scadoxus*, and *Cryptostephanus* Welw. ex Baker which are rhizomatous, amaryllids are typically bulbous perennial herbs that often must endure seasonally unfavorable conditions such as drought and or cold. Most bulbs respond to unfavorable conditions by initiating a period of dormancy, or rest. Amaryllids have two primary phases of growth (Traub, 1958). First

is the immature or vegetative growth phase in which rapid leaf production accompanied by root and stem production typically continues for 18 to 24 months. Second is the sexual reproduction phase in which the inflorescence(s) bear flowers. Ultimately, seed production is the result.

The tunicate bulb structure characteristic of Amaryllidaceae is a modified cone-shaped stem bearing leaves with modified leafbases. Most amaryllids exhibit a sympodial organization in the bulb. The bulb consists of two major components, the shoots and the roots (Traub, 1958). The shoot bears leaves, and inflorescences are initiated from the axils of the leaves. The contractile roots are fibrous in nature and formed in a ring from within the basal plate just below the point of attachment of the outermost, or lowermost leafbase or bulb scale). In *Hippeastrum*, the simplest true bulb type which lacks (true) scales but has modified leaf bases as storage organs, the bulb is comprised of several bulb units; in contrast, Narcissus has both both scale and leaf bases as storage organs (reviewed by Rees, 1992). In *Narcissus*, production of lateral bulbs units is more regular, albeit slower, but results in increased branching. The initiation of bulb units is proportional to the production of leaves. Each bulb unit consists of four leaves and the terminal inflorescence; the inflorescence is initiated from the axil of the innermost leaf and the bulb unit is in the axil of the next oldest leaf (Rees, 1992).

Bulblets are produced as a mean of asexual reproduction. The formation of offsets typically occurs at the region of root formation. However, in some taxa, bulbils are produced via rhizomes. In some species, bulblets may arise distally up on the keel of the bulb scale (Traub, 1958). From a study conducted by Yanagawa and Sakanishi (1980) on the morphology of bulblet formation from bulb scales in *Hymenocallis* Salisb. (Amaryllidaceae) and *Ornithogalum* L. (Hyacinthaceae), it was determined that bulblets arose predominantly from both the epidermal and subepidermal cells nearest in location to the vascular system. Interestingly, they did not observe any vascular connections between the bulblets and the mother bulb. Huang et al. (1990b) report that the connection of vascular bundles occurs between the newly formed bulblets and the abaxial side of the outer bulb scale. Dorsiventral polarity of regeneration in the Amaryllidaceae and Hyacinthaceae differs from the Liliaceae (Yanagawa and Sakanishi, 1980).

Traditional Amaryllid Propagation

A common practice in propagating amaryllis (*Hippeastrum*) and several other amaryllids is the cross-breeding of desired cultivars or species to pro-

duce new individuals with unique characters. Most amaryllids produce ample seed, although some amaryllids (e.g. *Calostemma* R. Brown, *Griffinia* Ker-Gawl., *Haemanthus* L., *Proiphys* Herb. and *Scadoxus* Raf.) produce only 3–4 ovules per locule with a total of three locules per capsule, typically resulting in only 1–3 seeds per cross. Another drawback to this method is that sexual reproduction of cultivars does not result in the production of true-to-type plants.

Cross-cutting and scooping have been traditional techniques applied to in vivo propagation of amaryllids. Cross-cutting the basal plate from below into 6–8 sections deep enough to fatally damage the apex of the shoot, or diligently scooping out the basal plate induces the production of bulbils.

Bulb scaling is another means of vegetative reproduction. Based on knowledge dating back to at least the 14th century, each scale detached and planted potentially will generate a new plant (Rees, 1992). Addressed here are two variations on this theme. In the first, in vivo propagation of twin scales, also termed fractional scale-stem cutting, developed by Traub (1933, 1934, 1935, 1958) and also Heaton (1934, 1935, 1936), leaves and roots are cut back to the bulb and then the bulb is cut vertically into up to 16 sections. Second, the bulb-scale method (Luyten 1926, 1953) is a process in which adventitious bulblets are formed via production of protuberances on the proximal basal plate end between the two bulb scale pieces (Okubo et al., 1990 and Huang et al., 1990a). The bulb-scale method, effective only on actively growing plants, is one whereby sprouting bulb scales are removed and placed in sand or vermiculite-filled flats. Bulblets are removed after a few months and transplanted.

In Vitro Propagation Methods

An exhaustive review of tissue culture of ornamental geophytes can be found in Kim and De Hertogh (1997).

The first consideration in culturing amaryllids in vitro is that the bulbs to be used for culture should not be in a dormant phase. Preferably, the bulbs should have recently emerged from dormancy. The most common in vitro technique applied to amaryllids is the propagation of bulb scale segments, resulting in bulblet formation. Both twin scales and single scales are used, depending on the species being cultured.

In both single and twin scaling, bulblets were formed from protuberances initiated at or near the point of attachment on the abaxial side of the scale proximal to the basal plate. In the single scaling method, protuber-

ances which developed into protocom-like bodies (Huang et al., 1990b) were induced on the abaxial surface at the junction of the scale piece and basal plate. Perhaps these protuberances should have been more accurately termed "protobulblets". In the twin scaling method, bulblets are formed directly from protuberances without an intervening "protocorm" stage. The term "protocorm" is used because, according to Uesato (1978), their structure and growth habit are quite similar in respect to the protocorms of orchids, to whose vegetative multiplication an analogy can be drawn. (Huang et al., 1990) The fact that a single bulb scale without the basal plate and connective tissue has the potential to give rise to new organs in vitro, as observed and reported by Oyamada (1974), is evidence for yet another method of in vitro propagation of amaryllids. Evidence for this would be the production of "protocoms" without an intervening callus stage, followed by the production of bulblets and shoots. However, in the literature, formation of protocorm-like bodies is not referred to as morphogenic, or embryogenic (somatic), despite the fact that the formation of protocorm-like bodies seems to arise through a process similar to that found in orchids (somatic embryogenesis). From histological sections, it appears that cell division occurs in epidermal and subepidermal cells on the abaxial surface of the scales. The progeny of these cells increase in size, resulting in a structure termed a protocorm-like body (Huang et al., 1990b). After two months these organized structures demonstrated differentiation and development of vascular bundles.

In the family Amaryllidaceae, twin bulb scaling is the preferred method of propagating *Hippeastrum* (Huang et al., 1990b), *Nerine* Herb. (Pierik and Ippel, 1977) and *Narcissus* L. (Hanks and Rees, 1978). Huang et al. (1990b) state that single scaling of *Hippeastrum* and *Hyacinthus* L. (Hyacinthaceae) is an inferior method of propagation. Hussey (1975) and Yanagawa and Sakanishi (1977) reported adventitious bulblet formation at the point of attachment of the scales to the basal plate of *Hippeastrum*. Their findings were in accord with those of Pierik and Ippel (1977) in *Nerine*, Hanks and Rees (1978), and Squires and Langton (1990) in *Narcissus*. In single scaling, bulblets were not directly formed; protocorm-like bodies were instead formed. In contrast, twin scaling of *Hippeastrum*, *Narcissus*, *Nerine*, and *Hyacinthus* results in bulblets forming directly without formation of protocom-like bodies.

O'Rourke et al. (1991) claim that a theoretical 250-fold increase over the numbers of plants resulting from the scale stem fraction method of cutting is possible with in vitro twin-scaling. Each bulb that was cut into scale stem

fractions, with the new bulblets formed subsequently quartered, produced ca. 100 bulblets each. This could be repeated every 10th to 12th week, resulting in a theoretical yield of 25,000 bulblets per year. This represents a dramatic increase in number over the method outlined by Huang et al. (1990a) and Tombolato et al. (1994), which require that the bulblets develop for at least a few years before offsets are produced.

Single scaling has proven efficient in *Lilium* L. (Liliaceae) and has also been shown to be the more effective method of propagating the amaryllid Amazon Lily, *Eucharis amazonica*, as reported by Pierik et al. (1983). In their experiment, explants were approximately 2.5 cm long and 0.75 cm wide with a 3 mm thick portion of the basal plate. Their study showed that inverting bulb scales when placing them on the media resulted in increased bulblet production by a ratio of 2.5 : 3.0. The excised bulb scale segments initiated adventitious bulblet formation on the lower sides. Temperature was an important factor as well, 25° C, as compared to 20° C for *Nerine* and 21° C for *Hippeastrum* (O'Rourke et al., 1991a). Rooting and sprouting in *Eucharis* bulblets were strongly promoted by the use of the auxin indolebutyric acid (IBA) , which was not the case in *Nerine* and *Hippeastrum*.

In all of the literature reviewed for this paper, workers' results clearly indicate that large scales (ca. 2.0 cm long) yield greater number of bulblets (Pierik and Ruibing, 1973; Pierik and Post, 1975; Hanks and Rees, 1978). Pierik and Post (1973) also reported that the number of bulblets formed in *Hyacinthus orientalis* is proportional to the length of the explants. Hanks and Rees (1978) report similar findings in *Hippeastrum* as did Pierik et al. (1983) in *Eucharis*. Okubo et al. (1990) attributes this to the degree of food reserves in the scales. Jacobs et al. (1992) found that twin-scale explants of Nerine oriented apolarly on the medium produced bulblets more readily and with higher fresh weight than those situated polarly. Using liquid shake culture, Bergoñón et al. (1992) found similar results with *Narcissus*.

Another method for tissue culture of amaryllids has been presented by O'Rourke et al. (1991c). Various floral tissues of *Hippeastrum* were examined for their ability to produce plantlets (bulblets) via callus (direct organogenesis) from floral tissue. One of the primary advantages of using floral tissue is that the bulb is not destroyed in the process, as is the case with scaling. This is especially important when working with extremely valuable or rare species. Tissues utilized as explants included floral scapes (peduncles), pedicels, petals, anthers, filaments, styles, and ovaries. The results varied in success. Petal tissue resulted in a three-fold increase in size after more than 9

months, but no plantlets formed. Anther and style tissues produced a yellowish callus that could not be multiplied, as was also reported by Bapat and Narayanaswamy (1976). Pedicel and ovary tissue explants initiated plantlets after a period of 32 weeks in culture (O'Rourke et al., 1991c). Plantlets formed on pedicel explants from the inner tissues at the proximal ends of the explants. With ovarian tissue, plantlets developed on the ovary wall and on the placentae (O'Rourke et al., 1991c). Lilien-Kipnis et al. (1992) presented a successful method for proliferation of *Nerine* somatic embryos in liquid culture using explants derived from inflorescence tissue.

A concern with this technique is the extended period required to initiate explants. Genetic instability and culture contamination increase proportionately with time. O'Rourke et al. (1991c) reported off-type plants obtained from pedicel tissues of *Hippeastrum* 'Pinksterflower' in 1976. The explants were cultured on a high salt NIS mediun supplemented with 2,4-dichlorophenoxyacetic acid (2,4-D) at 2 parts per million and kinetin (K) at 1 ppm. According to O'Rourke et al. (1991) these plants flowered routinely each year since 1979. The two off-types observed either produced a much smaller flower than the original clone, or were smaller plants overall.

It should be noted that the outermost bulb scales often produce contaminated cultures. This was reported by Huang et al. (1990b) and their suggestion was to discard the outermost bulb scales prior to culturing. From personal experience culturing *Eucharis amazonica* in vitro, I found that this is a wise precaution. Contamination in my experiment was approximately 35%.

Recovery of *Hippeastrum* mosaic virus-free subclones via shoot apex culture was reported by Nowicki and O'Rourke (1975). Shoot apices were excised from bulb cuttings and placed on filter-paper bridges in an artificial medium consisting of a modified Murashige and Skoog (MS) liquid nutrient medium (as defined for asparagus shoot-apex culture). Twenty-two months later, a significant number of plants remained virus-free.

Few studies report on the relative success of transferring micropropagated plant material to the greenhouse from culture. Transfer of *Eucharis* was characterized as difficult by Pierik et al. (1983). They found that inducing a short period of dormancy in the bulblets after removal from culture increased survivability as well as subsequent leaf production.

THE ROLE OF PLANT GROWTH REGULATORS IN AMARYLLID CULTURE

An in vivo experiment conducted by Tombolato, et al. (1994) using twin scaling, demonstrated that bulblet production of *Hippeastrum* was reduced in the

presence of auxins. Liquid IBA, indole-3-acetic acid (IAA) and 1-naphthalene acetic acid (NAA) were applied independently. The highest rate of bulblet production in the presence of any auxins was found in the treatment with IBA, however, highest bulblet production occurred with no hormone treatment.

Huang et al. (1990) tested various combinations of plant growth regulators on in vitro culture of *Hippeastrum*. Their experiment also showed that bulblet production increased in the absence of hormones. The two auxins used were IAA and NAA, and benzyladenine (BA), K, and zeatin (Z) were the three cytokinins used. Treatment with an application of 5.0 mg/l of K resulted in average bulblet production of 2.0 bulblets per twin scale. The cytokinin Z proved to be the most effective hormone in bulblet production, producing an average of 3.6 secondary protocorm-like bodies per twin scale.

O'Rourke et al. (1990a) concluded that the addition of hormones to the media did not produce my significant increase in their growth rates or their production of new bulblets, but that the addition of auxins from 1.0 to 5.0 mg/l slightly enhanced root production. Skoog and Miller (1957) reported that auxins and cytokinins play a role in plant morphogenesis. However, in many bulbous plants it appears that the modified leaf bases in the bulb contain sufficient nutrients and hormones necessary for multiplication. Protocorm-like bodies of *Hippeastrum* were obtained from single scales after two months' incubation on hormone free Murishage and Skoog (MS) medium (Huang et al., 1990b).

Various studies have been conducted on the effects of growth hormones on bulblet formation and the overall results are that hormone-free media stimulates greater number of bulblets to form in amaryllids (Huang et al. 1990a, 1990b; Tombolato et al., 1994). The protocorm-like bodies then formed bulblets and shoots with vascular tissue connecting to the vascular system of the protocorm-like body after about three months' incubation (Huang et al., 1990b).

Huang et al. (1990b) suggest the production of protocorm-like bodies via single scaling as a new method of in vitro propagation. Multiplication of "protocorms" is acheieved in liquid MS medium with 1.0 mg/I Z, then bulblet and shoot formation from "protocorms" in liquid MS medium with 1.0 mg/l IAA and 1.0 mg/l Z. Zeatin was the only cytokinin that was effective in stimulating secondary, or adventitious, protocorm-like bodies.

For the system of culturing floral tissue in vitro (O'Rourke et al, 1991b), explants responded most positively to optimal NAA and BA concentrations of 2.0 and 5.0 mg/l, respectively.

FUTURE WORK

The greatest obstacle to success of in vitro culturing of amaryllids is the limited demand for plant material. Attention must be given to further stimulate interest in this group of elegant bulbous plants. Further investigations into the role and effects of cytokinins in stumulating bulblet production may offer greater insights on how to increase amaryllid bulblet production in vitro. A limited amount of information about the internal morphology of bulbs has been compiled (Aksenkova and Sedova, 1981; Arroyo, 1984; De Hertogh and Le Nard, 1993; Müller-Doblies, 1977; Müller-Doblies and Müller-Doblies, 1972, 1978, 1985; Rees, 1992). More detailed comparative studies of bulb morphology might provide a better understanding of which groups of amaryllids would be better suited for propagating via either single scaling or twin scaling. Investigations into the in vitro multiplication of bulbils produced via rhizomes may provide an additional application. Once an efficient system of in vitro culture of amaryllids has been established, the horticultural industry should see the production of a wider array of exotic amaryllids and the selection for more vigorous, pest/pathogen-free bulbs.

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AMARYLLIS BELLADONNA, REGINAE AND *CAPENSIS*

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The most vulgar eye is struck with the beauty of this plant, and it very well deserves the title of elegant; its proper name is Amaryllis . . .

—*John Dicks,* New Gardeners Dictionary, *1771.*

In the *Hortus Cliffortianus* of 1738, Linnaeus described the West Indies Red Lily as *Amaryllis spatha multiflora, corollis campanulatis aequalibus, genitalibus declinatis.* He cited other descriptions and plates which are undoubtedly of the plant now called *Hippeastrum puniceum.* The same plant was then given the "trivial name" *Bella donna* in *Species Plantarum* of 1753, a name which was previously associated with this plant by Hermann, Plukenet and Tournefort.

Unfortunately there was confusion in England that led some writers, particularly those working near London, to claim that Cape Belladonnas were collected by Hans Sloane in Barbados. Linnaeus cited Sloane's description, which allowed the English writers to conclude that he meant to describe the [Cape] Belladonna lily. How Linnaeus could have overlooked every valid reference to the Cape plant while unerringly selecting only descriptions and plates of the American Belladonna has never been satisfactorily explained. Sealy (1939) claimed that Linnaeus saw a purple-flowered Cape Belladonna in George Clifford's garden (Holland), but confused it with Maria Sibylla Merian's vivid orange *Lilium Rubrum.* This is no more preposterous than Sealy's claim that the Cape Belladonna has beard pads.

To support his fanciful argument, Sealy discussed an unlabeled specimen in the Clifford Herbarium (now in the British Museum), which is undoubtedly a Cape Belladonna. L.S. Hannibal has determined that the blank specimen agrees very well with a plant formerly common around Hayward, CA, which he identified as 'Rubra Bicolour'.

There is no evidence associating Linnaeus with the Clifford specimen. Linnaeus left Holland in 1738, while Clifford continued collecting and distributing exotic plants until his death in 1760. This alone is sufficient to raise doubt about accepting the specimen as Linnaeus's "working type" for *Amaryllis belladonna.* Furthermore, the blank specimen has the solid scape typical of the Cape plants. Two of the authors cited by Linnaeus (Hans Sloane and John Hill) mentioned the hollow scape of the American plant.

Clifford traded plants and dried specimens with other gardeners such as Philip Miller, the famous gardener of Chelsea. If Clifford had such a plant, no doubt he would have shared it with others. Yet there is no reported description of the plant in the 1730s. The earliest published description I can find that agrees with the Clifford specimen is in the *Gardeners Dictionary* of 1759. This plant became *Amaryllis capensis* in the 1768 edition, even though it was not the plant Linnaeus described. Martyn apparently borrowed the epithet from *Lilio-asphodelus capensis Pet. gaz.*, which L'Héritier included under his *Amaryllis belladonna* (non L).

Miller wrote: "12. *AMARYLLIS spatha triflora corollis campanulatis aequalibus genitalibus declinatus.* Lily Daffodil with three Flowers in each Cover, whose Petals are equal and Bell-shaped, with declining Stamina." He continued "The twelfth Sort is also a Native of Africa, I received the Roots of this from the Cape of Good Hope with the former [*Brunsvigia orientalis*]. This produces its Flowers in February and March. The Stems of this rises near two Feet high, and have commonly but three Flowers inclosed in each Sheath, or Cover. The Flowers are as large as those of the Belladonna Lily, and are of the same Form, growing erect, but of a deeper Red Colour."

Also in the 1759 edition Miller first described a new strawberry (*Fragraria ananassa*) which he had recently received from Clifford. It is reasonable to suppose that Miller sent the new plant to his friend Clifford, since they were still trading plants. And it is unreasonable to claim that Linnaeus saw a plant before 1738 that was not imported until the late 1750s. Which is to say that the Clifford specimen could not have been the "working type" for *Amaryllis belladonna*, and we are not obliged to suppose that Linnaeus could not distinguish purple from orange.

Sealy's 1939 article contains factual errors and baseless speculations, which suggests he felt confident that the readers of the *Kew Bulletin* would not bother to check his sources. Sadly, even Sealy's critics failed to check some of the statements. For instance, L'Héritier gave the name *Amaryllis belladonna* to the Cape plant, as Sealy reported, but did not quote Linnaeus as authority for the name. L'Héritier cited *Species Plantarum editio secunda* (1762) and the *Gardeners Dictionary* (1768) for some of the species in his *Sertum Anglicum*, such as *Amaryllis formosissima* L., but these sources are conspicuously absent from the references under *Amaryllis belladonna* and *reginae*.

To trace the nomenclatural history of *Amaryllis belladonna*, we must go back to the *Hortus Farnesianus* of 1625. Among the exotic plants described, many of them American, was the *Lilionarcissus rubeus indicus*, also called

Narcissus Jacobeus for its fancied resemblance to the sword/cross emblem of the St. Jacob Knight (Equitum). Tobia Aldinus noted that the *Narcissus Jacobeus* of Clusius had a different appearance. Pietro Castelli's fine plate shows clearly that this plant was of the type that would later be identified by Linnaeus as *Amaryllis belladonna*. Aldinus described the color as "rubra", "rubeus" and "rubicundissime".

Ferrari also described this American plant in his famous *Florum Cultura* of 1633. His description agrees with that of *Hort. Farn.*, and adds a few details. He described the color as "*purpura in crocum languente*", red with pale yellow. (The purpura dye varied in color from blood red to rich violet). It bloomed in May or June. Immediately following this description, Ferrari wrote about "another Indian narcissus" that was "rarer and nobler", and only recently introduced. This was the plant we now call the Cape Belladonna.

The confusion between the American and African plants apparently began when Plukenet (1696), working in London, mistakenly supposed that the *Hort. Farn.* plant was a Cape Belladonna. He listed Morison's name for the Cape plant, *Lilio-Narcissus Indicus saturato colore purpurascens*, with *Lilio-narcissus rubens indicus. Aldini, Hort. Farnes.* as a synonym. It is interesting to note that Plukenet did not assign the name "Belladonna" to this entry, but reserved that for Hermann's *Lilium Americanum puniceo flore Bella donna dictum*, which he renamed *Lilio-narcissus Americanus puniceo flore Bella donna dictus*. Northern botanists, aside from Barrelier (pub. 1714), generally referred to Ferrari's Latin edition (first published in 1633) rather than the Italian of 1638, in which he used the name Belladonna. The Latin edition was reprinted in Amsterdam in 1664. John Rea's English translation came out in 1665, and again in 1676 and 1705.

In addition, Plukenet misspelled "rubeus" as "rubens", which altered the color value. *Rubeus* was traditionally used for the red of domesticated animals, whereas *rubens* was merely red. [L'Héritier and De Candolle later copied the incorrect spelling when they included *Lilionarcissus rubens indicus* under their *Amaryllis belladonna* (non L). Apparently they trusted Plukenet, and failed to examine *Hort. Farn.* for themselves.]

Other writers of the period, such as Hans Sloane and John Ray, regarded Plukenet as unreliable. Thus his misidentification went apparently unnoticed until the 1740s when artist George Ehret, also in London, initiated a new phase in the confusion.

Ehret's watercolor sketch of the American plant is labeled *Lilio-Narcissus Indicus saturato colore purpurascens, Moris. Hist.* and *Amaryllis spatha multi-*

flora corollis campanulatis aequalibus genitalibus declinatus, Linn. h. Cliff. In this he copied Plukenet's synonymy, substituting Linnaeus's phrase name for Aldinus's.

Further proof of Plukenet's influence can be seen in Ehret's 1744 painting of a pink and white Cape Belladonna labeled *Lilio-Narcissus Americanus Belladona dictus par. bat.* This is the wrong name for the plant, of course, but is also the wrong source for the name. Hermann's phrase-name for the American plant is *Lilium Americanum etc.* in the *Paradisus Batavus.* It was Plukenet who changed the name to *Lilio-narcissus.* Furthermore, Plukenet actually quoted the *Prodromus* which does not contain Hermann's plate of the American plant. Ehret saw Linnaeus for the last time in 1737, and their letters were few and far between. It is unreasonable to claim (as some have done) that Linnaeus shared Ehret's new opinion.

One might suppose that Sir Hans Sloane, who collected the Red Lily in Barbados, would have had something to say about his description of that plant being applied to something quite different, but I have found no comment on the matter that can be attributed to Sloane. He was apparently a meticulous botanist, but was otherwise notorious for his fanciful stories (e.g. his claim to have a straw hat once owned by Pontius Pilate's wife's sister's handmaiden). Peter Collinson (20 March 1745-6), who knew or corresponded with many other botanists and gardeners (including P. Miller, Sloane, Ehret, Linnaeus, Solander) wrote to Jakob Trew about "the Red Mexico Lilie (vulgo). But they are found in all Our Islands and are undoubtedly what Sir Hans Sloane mentions in his History of Jamaica." He, at least, did not accept the myth of Cape Belladonnas in Barbados.

In the *Gardeners Dictionary* of 1731 and 1741, Philip Miller described the Red Lily of the West Indies with Sloane's phrase-name, *Lilio-Narcissus polyanthos, flore incarnato, fundo ex luteo-albiscente,* with no hint of confusion. By the 1750s things had changed. The Red Lily was identified in 1754 as *Amaryllis spatha multiflora, foliis ovato-oblongis obtusis. Flor. Leyd.*, which is actually *Brunsvigia orientalis* (L) Heist. The Cape Belladonna was then identified as *Amaryllis spatha multiflora, corollis campanulatis aequalibus, genitalibus declinatis. Lin.*

In 1755 Miller published the first edition of *Figures of Beautiful Plants,* which contains plates of the rival Belladonnas. Miller wrote that the [Cape] Belladonna lily "is said to be gathered by Sir Hans Sloane, in the Island of Barbados; and his Description seems to be well enough adapted to this Plant; but from all the Intelligence I have been able to procure from the

Inhabitants of the several American Islands, they have but Two Species of what they call Lilies; One White, which is a Pancratium [Ed. Note: now *Hymenocallis*], and the other Red, which is what I have before mentioned, and is a very different Species from this."

Miller went on with a bewildering discussion of three species supposedly native to the islands of the West Indies, though he could verify the existence of only one. Sloane cited Du Tertre and Hermann, but Miller claimed that each had described a distinct species. Without pictures the discussion would make even less sense. Accidentally or not, in the 1760 edition of *Figures* the plates were reversed and renumbered from the 1755 editon, though there is more to the confusion.

Miller associated the Cape plant with Sloane's and Linnaeus's phrase-names, though Sloane had described the hollow scape of his plant, and Linnaeus cited Maria Merian's vivid orange *Lilium rubrum*. Merian also cited Sloane and Hermann. Du Tertre's Red Lily was described by Miller as "*marginibus reflexis*". Miller distinguished Hermann's *Lilium Americanum* as "*marginibus undulatis*", and identified it with the *Lilium Reginae* of Douglas. However, t. 23, the American plant, is labeled *Amaryllis spatha multiflora corollis campanulatis* ***marginibus reflexis*** *genitalibus declinatis*, which was Miller's name for Du Tertre's Red Lily. The text of Plate XXIV refers to Hermann's plant, which Miller called *Amaryllis spatha multiflora, corollis campanulatis aequalibus,* ***marginibus undulatis.*** Apparently not the same plant.

Linnaeus is known to have had the *Gardeners Dictionary* of 1759 (no relevant pictures) and *Figures* of 1760. In his *Species Plantarum 2nd* (1762) Linnaeus accepted Miller's plates and descriptions as printed, which explains how Hermann's plate came to be cited as an illustration of *Amaryllis reginae*. The *Gardeners Dictionary* of 1768 (Prof. Martyn's edition) was the first edition of that work to employ the binomial system throughout. This work agrees with *Species Plantarum 2*, except that Hermann's plant was placed back with *Amaryllis belladonna*. Confusingly, Sloane and *Hort. Cliff.* are still associated with the Cape plant, which was identified as *Amaryllis reginae*.

In 1783 Lamarck followed the *Gardeners Dictionary* (1768), but referred only to Morison's phrase-name, and plates of the Cape plant for *Amaryllis reginae*, which he renamed *A. rosea*. He acknowledged that *Amaryllis Belladonna* L. was not the "true Belledame of the Italians", then changed the name to *Amaryllis punicea*.

Meanwhile, John Hill added further color and confusion to the story. In 1751 he listed the Jamaica Amaryllis with red and yellow flowers in his

General Natural History. His *Outlines for a System of Vegetable Generation* (1758) contains excellent and detailed plates of the American plant, which he identified as *Amaryllis Spatha multiflora, corollis campanulatis aequlibus, genitalibus declinatis- Linn. Sp. 293*. Clearly, Hill knew which plant Linnaeus had in mind.

Hill admired Linnaeus's system, but was not a slave to it. Earlier (1756) he had reinstated some genus names (*Cymbalaria, Petroselinum, Levisticum*) that Linnaeus had banished. In his *Vegetable System* (vol. 25, 1774) Hill wrote of *A. reginae* "They resemble the Bella Donna extremely; but there is an absolute and fixed difference: the Petals in this are waved at the edge, and strait at the base; whereas the Petals of the Bella Donna have a bend at the base, and are strait at the edges." This is in agreement with Linnaeus's descriptions, and was confirmed when Linnaeus cited Hill's 1758 plates in *SP2* (1762) and in *Mantissa Plantarum* (1767 & 1771) as illustrations of his *Amaryllis belladonna*.

Also in *Vegetable System*, Hill identified the Jamaica Amaryllis as *Amaryllis biflora*. He did not mention a cream-colored form of the Jamaica Amaryllis, but in the previous year Rottböll assigned the name *Crinum biflorum* to a species that seems to be *Amaryllis dubia* Alm (= *Crinum barbatum* Linn. Herbarium. Disagreement over the distinctions between *Amaryllis* and *Crinum* continued well into the 19th century. Linnaeus transferred *Amaryllis zeylanica* to *Crinum* as early as 1767, but John Lindley continued to disagree in 1821. It is not surprising that two of Linnaeus's students would differ regarding a dried specimen. The name *Amaryllis biflora* (Rottböll) Hill, would have priority over Lamarck's *A. punicea*, though of course *Amaryllis Belladonna* L. (1753), Mill. Dict. (1768) and Hill (1768) are even earlier.

In Hill's *Hortus Kewensis* of 1769, *Amaryllis belladonna* was listed but not described. *Amaryllis reginae* was not mentioned at all. He also listed *Amaryllis gutatta*, which indicates that he was not referring to *Species Plantarum 2* (1762) where that name was changed to *A. ciliaris*. Since he correctly identified *Amaryllis belladonna* in 1758 and 1774, it is safe to assume that *A. belladonna* Hort. Kew. (1768) was the same.

Linné the younger visited Kew after his father's. He renamed the Merian's plant *Amaryllis equestris* perhaps alluding to the fact that his father was a knight of the Swedish Royal Order of the North Star (a title Linn. fil. inherited when his father died). The emblem of the Order was a cross with a 5-pointed silver star in the center. The name was published in Hortus Kewensis 1789 though the alternative spelling, *equestre*, is sometimes found.

He distinguished this species by its horizontal filiform tube, whereas his *Amaryllis reginae* had a short, nodding tube. He referred the latter name to the West Indische rothe Lilie of Seligmann, which is similar to Hill's plates of 1758. This explains Sealy's sly assertion that Hill's plant was actually *H. reginae* (Herb.). True enough, but it was not *Amaryllis reginae* L.

Writers of various countries continued to accept that Linnaeus had described the American plant, even some in England. John Dicks (1771), gardener to the Duke of Kingston, described the American or Crimson Amaryllis—translating Linnaeus's Latin phrase-name—and even gave instructions for collecting the bulbs in their native land. He noted that they bloomed in September in America, and had trifid stigmas. The color was "a fleshy crimson, and in the center there is a large circle of yellow, terminated every way by a kind of rays". This is not a perfect match for Merian's *Lilium Rubrum*, but is certainly closer than any variety of Cape Belladonna. It agrees very nicely with Ehret's painting. Aublet (1775) reported finding both *Amaryllis Belladonna* and *reginae* in French Guyana. Vellozo (1790) depicted *Amaryllis bella-dona* (similar to the plate in Miller's *Figures*) but commented that the plant should be called "quadriflora" rather than "multi-flora". His Brazilian plant bloomed in August and September.

Ruiz & Pavon (1802) had a narrower view of species than Dicks. They commented that their *Amaryllis miniata* was closely akin to *A. belladonna* (*Affinis est Amaryllidi belladonae Linnaei*), but distinguished it by several characters.

De Candolle, in Redoute's magnficent *Les Liliacées*, commented that *Amaryllis equestris* properly deserved the nick-name *Belladonna*, but he preferred to respect the received terminology. De Candolle was also associated with the Banksian school at Kew, but was less constrained in France than the English writers.

Mrs. Bury's *Selection of Hexandrian Plants* followed the Kew terminology in general, but the description of *Amaryllis reginae* contains some surprises. She wrote "the following correct description is taken from Professor Martyn's edition of Miller's Dictionary, published in 1768 'Bulb green, scape round, sub-compressed. Each stem supports two, three, or four flowers, rarely more; they are large, of a bright copper-colour inclining to scarlet, with a bottom of a whitish green; the three outer petals reversed at the tip, the three inner fringed at the base; the style red: the spathe which covers the buds before they open, divides into two parts to the bottom, standing on each side the umbel of flowers. '"

She failed to mention that the "correct description" was actually published under *Amaryllis belladonna*. In addition, the phrase "the three outer petals reversed at the tip, the three inner fringed at the base; the style red" is not found in the *Gardeners Dictionary*, but is an approximate translation of Linnaeus's "Petala 3 exteriora intus apice ungue reverso. Petala 3 interiora basi ciliata. Stamina declinata, rubra", from the *Mantissa Plantarum* (1767 & 1771) description of *Amaryllis belladonna*.

John Lindley provided a clue in his *Vegetable Kingdom*, where he informed us of Endlicher's report that the bulbs of *Amaryllis Belladonna* were used in the West Indies to poison arrow tips. Lindley commented that this must be an error, and that a *Hippeastrum* was probably so used. Endlicher knew which plant Linnaeus had described.

William Herbert separated the Cape Belladonna from *Amaryllis*, combining it with Heister's *Brunsvigia* in the new genus *Coburghia*. Richard Salisbury objected, claiming without evidence that Linnaeus founded the genus *Amaryllis* on the "Belladonnum" of the Italians. Linnaeus actually took the name from Hermann. John Lindley also objected, but on the grounds that Herbert was creating artificial genera.

Herbert recanted, but did not accept Salisbury's claim that the Cape Belladonna was described in *Hort. Cliff.* when *Amaryllis* was first published. He allowed that the Cape Belladonna was not growing in Clifford's garden, which alone invalidates Herbert's *Hippeastrum*. As E. D. Merrill wrote "It is to me inconceivable that a genus proposed by one author should be interpreted by others with every original species excluded." This also applies to Herbert's interpretation of *Brunsvigia* without Heister's type species.

Herbert wrote "I therefore restored the name *Amaryllis* to Belladonna, and gave that of *Hippeastrum* or Equestrian star to this genus, following up the idea of Linnaeus when he named one of the original species equestre." Linnaeus did not name any species "*equestre*".

Herbert made so many obvious errors that he may have wanted the truth discovered. Even the name *Hippeastrum*, or Equestrian Star, alludes to Linné the knight. Herbert continued "Mr. Sweet was perhaps misled by knowing that equestre, which is one of the plants described, was called belladonna by Merian; but Merian only called it *another belladonna*, with reference to the plant of the Italian gardens, thinking erroneously that it was of the same genus. Barrelius had previously, in the year 1714, described the pink and white belladonna, as cultivated by that name in the gardens of Italy, and to the plant of Barrelius both Merian and Linnaeus alluded."

Merian did not call her Red Lily "another belladonna". She only cited Hermann's phrase-name. Writing in 1705, she could not have known about Barrelier's work, unpublished until 1714. And why would a woman just returned from a perilous voyage to Surinam have Italian gardens in mind? Coincidentally, Heister (1753) wrote that Merian had depicted Ferrari's plant. However, it was another Merian — her father, Matthäus — and a different plant — *Brunsvigia orientalis* (L.) Heist. This may account for Miller's 1754 misidentification, and suggests that Herbert was planting clues. Ferrari, Barrelier, Linnaeus and Merian failed to mention anything about the female complexion. Herbert continued, "To suppose he would have alluded to a bright orange flower would be perfectly absurd."

It is well known that Hermann did give the name "Bella donna" to an orange (scarlet) flower, and was followed in this by Plukenet and Linnaeus. Perhaps Dean Herbert was slyly alluding to Dean Swift's well-known aversion to red haired women. Otherwise Herbert's argument is merely absurd.

AMARYLLIS AND BELLADONNA

Plukenet's *Lilio-Narcissus Indicus, s. Narcissus Liliflorus aureus striis, argenteis pictus, floribus amplis cernuis gemellis, caule magno Cepae fistuloso*, which Lamarck renamed *Amaryllis striata*, was already established in some European gardens before 1700. Miller had this plant in 1731, and translated the name "Indian Lily-Daffodil with ample Gold-coloured flowers spotted with silver, and a large hollow stalk."

Gold, in Portuguese, is "amarello", which becomes "amarellas" in plural. Due to the ambiguity of color words, gold could mean yellow or orange. Mrs. Bury's painting of *Amaryllis crocata* is light, bright orange, though it has been called yellow. "Crocum" (saffron, yellow or gold) is similarly ambiguous. Ferrari described the 4-flowered Jacobeus as "purpura in crocum languente" (red with pale yellow), while Patrick Browne (1789) called the Jamaica *Amaryllis* "Flore croceo", gold-flowered. A plant with lily-like orange flowers, collected in Portuguese Brazil, could have been called Lirios amarellas — Amarellas lilies — particularly if collected by gold prospectors. Linnaeus commented that gardeners called the plants Amarellas or Amaryllis. Similarly, *Hemerocallis fulva* was called "red" or "scarlet" or "orange" by various writers of the 17th and 18th centuries.

Ira S. Nelson (Herbertia, 1955) reported that the Aymara girls of Bolivia formerly used the juice of amaryllis bulbs to give color to their cheeks. "For one night their complexion would glow with radiant beauty. In the several

days that followed, however, they would have to remain out of sight of their lovers because their cheeks would be drawn, cracked and as rough and ugly as they had been glamorous on the night the juice was applied. One of the older women summed it up by saying 'thank God for Max Factor.'" John Hill (1767) also reported "Fairwort" as a common name for *Amaryllis*, which suggests some knowledge of the ancient practice. At least three books on the Aymara language, including a dictionary, were published in Rome by 1613. Aldinus also mentioned the *Cruce Triumphante* of Bosius and Cieza's *History of Peru*, which deal with the same region. The *Lilionarcissus rubeus indicus* may well have come from Peru or Bolivia, along with ethnobotanical information about its uses.

SUMMARY

The confusion regarding the American and African Belladonnas was primarily an English phenomenon. It can be traced from Plukenet (1696) to Ehret (1744), and then to Miller. From the 1750s onwards, it was established at Chelsea and beyond that Sir Hans Sloane had collected Belladonna lilies in Barbados. No doubt Ehret's popularity as a painter and botanical demonstrator contributed to the spread of the error around London.

By 1755 Philip Miller expressed his doubt about the American origin of the Belladonna lily. He had received a white flowered plant from the Cape of Good Hope (via Holland) in 1754 which differed from the Belladonna lily only in color. By 1759 he also had a red flowered Cape plant which resembled a smaller, darker Belladonna lily. Even so, as late as 1804 John Sims wrote in the *Botanical Magazine*, "The channel through which the plant has been received makes it more than probable that it is a Brazil vegetable."

De Candolle admitted that *Amaryllis equestris* was the *belladonna* of Linnaeus. Lindley knew, but only dropped cryptic hints. Herbert also knew, admitted that *equestris* was the plant described in *Hort. Cliff.*, then argued so falsely about Linnaeus and Merian that he must have wanted the truth revealed.

Herbert's main concern was to unite the Cape Belladonna with *Brunsvigia* of Heister, which is justified by their reproductive affinity [Editor's note: crossability is not regarded as a paramount criterion for establishing generic delimitations by most modern botanists]. Unfortunately, by his time species very different from Heister's plant had been assigned to that genus by the Kew botanists. Herbert tried to establish a new genus, *Coburghia*, but was rebuffed for various reasons.

The name *Amaryllis* (from Amarellas) is possibly derived from the Portuguese "amarellas", which is "yellow" or "gold". A gold-flowered species was described by Plukenet (1696), and grown by Philip Miller in 1731. Patrick Browne described the Jamaica Amaryllis as gold-flowered (Flore croceo).

Juice of amaryllis bulbs was formerly used to redden the cheeks of Aymara ladies in Bolivia, which provides an ethnobotanical justification for the name *belladonna*. Plants matching the descriptions of *Amaryllis belladonna* L. are native to Bolivia.

Taken together, *Amaryllis* and *belladonna* are appropriate names for the American plant, as Linnaeus indicated when he labeled it *Amaryllis belladonna*.

The 17th century concept of species was rather broader than the current view. It is probable that several modern species were combined under the various published names. Bloom time is no help in identifying the various forms grown in England, in part due to differences in culture. For instance, Hill (1774) wrote that *Amaryllis reginae* L. bloomed in August, while Linn. fil.'s redefined version bloomed in January.

The *Hort. Farn.* plant may have come from Peru or Bolivia, and seems to agree with a Peruvian plant described by Bernabe Cobo [1580-1657]. Hermann's was from the Caribbean islands. Other forms came from Portuguese Brazil (diamonds were discovered there in 1725) which might account for plants with trifid stigmas. These new forms were imported in abundance, and were assigned to previously described species.

The *Amaryllis reginae* painted by Redoute does not resemble those depicted by Hill or Bury. The "West Indische rothe Lilie" of *Hortus Nitidissimis*, which Linné the younger called *Amaryllis reginae*, is generally recognized as *Hippeastrum puniceum* despite its short tube.

CONCLUSION

Amaryllis belladonna is the name given by Linnaeus to the American Belladonna, which he first described in *Hortus Cliffortianus*. This was recognized by contemporary and later writers from Holland (Royen, Seba), Spain (Ruiz & Pavon), Portugal (Vellozo), France (Aublet, Lamarck), Switzerland (De Candolle, Gessner), Bavaria (Endlicher), Denmark (Hornemann), and even some in England (Collinson, Dicks).

Amaryllis reginae L. remains ambiguous. Miller's *Dictionary* (1768) attached this name to the Cape Belladonna, which was accepted by Lamarck (1783). De Candolle also listed *A. reginae* L. under *belladonna* (L'Héritier non L), but was doubtful. Hill (1774) associated the name with an

American plant, which is possibly the current *Hippeastrum reginae* (Herb.), though there are discrepancies in the descriptions.

The confusion over the Belladonnas can be traced from Plukenet to Ehret, and then to Chelsea and Kew by the middle of the 18th century. An earlier phase of the confusion goes back to Parkinson's *Paradisi* (1629) through Rea (1665) and Morison (1680).

Amaryllis biflora Hill (1774) has priority over Lamarck's *Amaryllis punicea* (1783), but Miller's *Gardeners Dictionary* (1768) correctly identified the "Mexican lily" as *Amaryllis belladonna*, in agreement with Linnaeus (1753, 1762, 1767).

The blank specimen in the Clifford Herbarium does not fit Linnaeus's descriptions of *Amaryllis belladonna*, which had petals reflexed at the base, and beard pads. It does agree with Philip Miller's description of a plant received from the Cape of Good Hope in the late 1750s, and could not have been the "working type" for a plant described nearly 20 years earlier.

I would like to thank L. S. Hannibal for his encouragement and assistance. He provided invaluable information and photocopies of papers I would not otherwise have seen.

Editor's Note: It should be noted that the Committee on Nomenclature of the 1987 International Congress approved Peter Goldblatt's 1984 (Taxon 33: 511-515) proposal that the name *Amaryllis belladona* L. be conserved for the Cape belladonna, regardless of any future revelations concerning the "true" application of the Linnaean binomial.

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A NEW SPECIES OF *SPREKELIA* (AMARYLLIDACEAE)

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The cover of Plant Life (Herbertia) Vol. 26, 1970, is adorned with a drawing of a dwarf *Sprekelia* species which was collected by Dr. Thaddeus Howard at Puebla and Oaxaca, Mexico, in 1962 and 1963. Howard, who was awarded the Herbert Medal in 1970, discussed this new species in elaborate detail in his discourse on bulbous plants of Mexico and Guatemala published in the same volume. He remarked that it was not at all a rare bulb in his experience, but had likely been overlooked by previous botanists because its leaves resembled a *Zephyranthes* or *Habranthus* when not in bloom. In fact, when he first collected this dwarf *Sprekelia* in the sterile state, Howard wrote in his notes that he had collected an unknown *Zephyranthes*. Howard never formally published it as a new taxon. Other than his discourse in the 1970 Plant Life, the only other reference to this bulb was provided by Wilson (1975). Wilson (1975) reported that Howard had given her a bulb but that it had subsequently rotted over winter. She related recommendations from Howard on how to cultivate *Sprekelia* in her annual *Zephyranthes* report. She briefly mentioned a subsequent recollection in her 1983 bulb catalog, and planned to eventually offer bulbs of this "mini" *Sprekelia* for sale, but her untimely death interrupted this plan.

In 1989, I accompanied Howard and J. Kersey on a bulb collecting expedition into Northeast Mexico. On this occasion I experienced my initial sighting of *Sprekelia formosissima* Heist in bloom east of San Luis Potosi, capital of the state with the same name. These bulbs were growing in humus deposits that had collected in crevices on a rocky hillside. Howard remarked that finding bulbs of *S. formosissima* was becoming more difficult since they were highly prized as garden ornamentals. The subsequent year, Howard, Kersey, and I collected in Guatemala, and although we searched for indigenous *Sprekelia* in several promising localities, the only bulbs we managed to locate were growing in disturbed land adjacent to the highway.

In 1994, Howard, Kersey, N. Lehmiller and I flew to Acapulco and undertook a bulb collecting expedition in the State of Guerrero on the southern Pacific coast of Mexico. The trip began with a good omen: on the first day in the field, we found the presumed extinct *Hymenocallis astrostephana* Howard flowering alongside a small stream south of Chilpancingo. On the third day, we explored a semi-arid locality south of

Taxco. As I wandered along a sloping hillside partially covered with thorn bush and small trees, I observed occasional small bulbs in leaf that I presumed were *Zephyranthes*. Knowing that Howard was particularly interested in the small bulbous plants of Mexico, I dug several and presented them to him. Much to my surprise, he remarked that *Zephyranthes* did not occur in such a habitat, and what I had collected was likely a dwarf *Sprekelia*. Needless to say, I was silently skeptical about the tentative identity of a "dwarf *Sprekelia*. We did find this bulb in leaf once more near Taxco, again on a hillside. The following day near Iguala, we observed *S. formosissima* in leaf on a rocky ledge growing in humus. Before the trip was over, we had discovered two more *Hymenocallis* species which Howard thought were probably undescribed but required more study.

I cultivated the tentative dwarf *Sprekelia* bulbs in small clay pots. When winter came, I completely withheld all water, and the bulbs resided in a dry dormant state within my greenhouse for five months. None bloomed in the spring of 1995, but during the remainder of the growing season, several bulbs produced offsets. Then in the spring of 1996, three bulbs bloomed. Howard was indeed correct; these were dwarf *Sprekelia*. I successfully cross pollinated the flowers and obtained fruit and seeds, but when I applied their pollen to several flowers of *S. formosissima* which had simultaneously bloomed, no crosses took. Howard (1970) also was unsuccessful in cross pollinating the dwarf *Sprekelia* with *S. formosissima*.

It is with great pleasure that I formally describe and name this species in honor of Dr. Thaddeus Howard, whose contributions to our knowledge of the Mexican bulb flora are manifold.

Fig. 1. Side by side comparison of blooming *S. howardii* and *S. formosissima*, the latter collected near Iguala, Mexico.

Fig. 2. Comparison of pressed mature leaves of *S. howardii* and *S. formosissima*, the latter collected near Iguala, Mexico.

***Sprekelia howardii* Lehmiller; sp. nov. (Figs. 1-2)**

Species nova a statura minore et foliis *Zephyranthis simulans* a *S. formosissima* differt. Type: Mexico. State of Guerrero, south of Taxco. *Ex hort* Lehmiller, from bulbs collected 5 July 1994, and cultivated in Southeast Texas, 1996, *Lehmiller 1940* (holotype: TAMU).

Bulb ovoid, covered with a dark tunic, 15-20 mm diam, elongating into a slender underground neck 25-40 mm long. Leaves arising with the flowers or shortly thereafter, slender and lanceolate with a minute dorsal midrib, 17-26 cm long, 4-5 mm wide at base, 6-9 mm wide at the middle, dark bluish green but not glaucous, acute at the apex; at maturity becoming channeled, especially at the base and appearing nearly petiolate, with a fine longitudinal network of parallel nerves visible dorsally, margins smooth. Scape hollow, red at the base and light reddish green at the apex, 4-15 cm long; spathe erect at anthesis and clasped about the pedicel, persisting into fruit and remaining erect, but drying and turning dull red, 3-5 cm long. Pedicel erect, light reddish green, 25-45 mm long, elongating in fruit up to 55 mm long. Flower solitary, zygomorphic, and unscented, resembling *S.formosissima* but smaller in all dimensions; outer tepals wider then inner, 95 mm long by 11mm wide, upper tepal vertical and two lower tepals clasped against the stamens as the latter emerge from the throat; inner petals longer than outer and curved, 102 mm long by 6 mm wide. Stamens fasciculate, unequal, with the superior shorter, 80-95mm long; immature anthers purplish red, becoming black at maturity; pollen yellow. Style declinate, 105mm long, red, stigma weakly trifid. Ovary green, inclined at a 45 degree angle from the vertical, 7mm long by 5mm in diameter. Fruit a tri-loculicidal capsule, distinctly trilobed, initially green with a red flush, turning tan at maturity, 25 mm in diameter; seeds black, thin, D-shaped, 16-20 per lobe, arranged in two interdigitating columns within each lobe.

Habitat: Southern Mexico, states of Guerrero, Colima, Puebla, and Oaxaca, inland on the Pacific mountain chain at lower to intermediate altitudes, growing in dryer regions among small trees and thorn bush, usually on hillsides.

DISCUSSION

Baker (1888) treated *Sprekelia* as a monospecific genus with four varieties, but Howard (1970) considered *S. glauca* Lindley as a separate species particularly because of its glaucous leaves. Whether or not *S.clintiae* Traub (1965), another reported Mexican species with glaucous leaves, deserved separate speciation from *S.glauca* was not fully resolved by Howard.

Sprekelia howardii differs from the other species of *Sprekelia* by the combination of its miniature form and its leaf characteristics. Vegetatively, it is totally unlike the other species or varieties of *Sprekelia*. As leaves of *S. howardii* begin to emerge from the ground, they are alternately pressed flush against each other like those of *S. formosissima*, but soon thereafter the basal portion of each leaf becomes remarkably channeled. The latter effect, which creates a near petiolate appearance, causes each leaf to push away from the opposing leaf at the base, leading to an arching, sprawling pattern as the leaves assume a random orientation with respect to one another. The overall leaf configuration resembles *Zephyranthes* or *Habranthus*. Not only are the leaves slender, but they are also lanceolate, another character which differs from *S. formosissima* (Fig. 2).

Howard (Wilson, 1975) has already discussed the tedious cultivation requirements of this species, particularly the necessity for absolute dry dormancy during winter. Additionally, when potted the bulbs must not be disturbed; if repotted during the growing season, they will fail to flower the subsequent year. Other than representing a challenge to the enthusiast, this species appears to have limited horticultural value. The possibility of intergeneric crosses with *Zephyranthes* and *Habranthus* does warrant investigation.

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THREE NEW MILLA SPECIES FROM MEXICO

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Prior to Moore's (1953) monograph, only two species of the genus *Milla* had been described: *M. biflora* Cav. and *M. bryanii* I. M. Johnston. In his monograph, Moore described four new species: *M. magnifica*, *M. rosea*, *M. mortoniana* and *M. delicata*. *M. oaxacana* was described by Ravenna (1971). In the mid sixties, this author became aware that there were still a number of undescribed species in Mexico and Guatemala not included in Moore's monograph. Some of them had been erroneously determined as *M. biflora* from dried specimens, and the description for *M. biflora* was expanded to accommodate some of the nonconforming populations. These included forms from the states of Chiapas, Oaxaca and Guerrero in southern Mexico, and Puebla, Morelos and San Luis Potosi of central Mexico.

In his broad concept of *M. biflora*, Moore (1953) omitted mentioning the oblanceolate-ovate inner three perianth segments which so characterize *M. biflora*, allowing him to treat them generically as ellipsoid. This permitted the inclusion of other allied *Milla* having only ellipsoid segments, as well as other characters apparently unknown to Moore, such as strictly nocturnal flowering and stoloniferous rhizomes. With *Milla biflora* and *M. filifolia* the outer three segments are elliptic, while the inner three are broader, narrowing abruptly at the base, like an ovate spatula. This results in small open spaces at the base of the perianth segments, giving the illusion of tiny "windows" between the segments, where normally they would overlap. Night flowering *Milla* species have overlapping elliptic or ovate segments. Moore was unaware that some *Milla* species are strictly crepuscular, remaining closed throughout the day, opening at sunset and closing before sunrise. This explains why such showy plants were otherwise overlooked by botanists who observed closed flowers in the field during the day, misinterpreting them as *M. biflora*. In the evenings they did look much like *M. biflora* and this was not a surprise. The latter remains open night and day. Moore was unaware that certain *Milla* produced rhizomatous stolons at anthesis, terminating in new corms after anthesis (Moore, pers. comm.). Normally, specimens are collected at anthesis. He was aware of *M. magnifica* producing cormlets on short rhizomes, but again, this seemed of little importance. He was unaware that some *Milla* forms might produce cormlets on long, sometimes branching stolons, and that such stolons continued to elongate, and even branch, well after anthesis. Apparently no one bothered to

check them out, assuming that these were simply variations within *M. biflora*, or that the newly forming rhizomes were simply large roots. Since they do not fully develop until after anthesis, whereupon the stolon shrivels and decays, terminating in a new corm. Moore was also puzzled by discrepancies in the numbers of nerves of the perianth keels in geographical forms in his enlarged concept of *M. biflora*, but apparently decided not to make it an issue. As a result, several new species were unintentionally repressed for lack of understanding. The purpose of this paper is to tidy up those loose ends. In future work, new characters need to be incorporated to better differentiate the species, such as the basis of tepal form, whether or not the flowers remain closed throughout the day, and whether or not the plants form basally attached cormels, or cormels at the ends of stoloniferous rhizomes. Foliar and scape differences are important as to the presence or absence of denticulations, or minute pubescence, as are the numbers of nerves in the perianth keels. Chromosome numbers are useful too, if known (Lenz, 1971).

Milla mexicana T.M. Howard sp. nov. (Fig. 1).

Milla magnifica affinis sed differt cormo parvo, faciens rhizomatis elongatum, foliis angustatioribus, scabridiusculioribus, septem nervatis, leviter parvioribus. Differt a *M. biflora* floribus nocturnis, tepalis ellipticis. clausus die cormo fasciens rhizoma.

TYPE: *Howard 62–44* (holotype: MO).

Corm solitary, or one of a cluster, 2–2.5 cm diameter, 1.5–2 cm high with a collar 2.4 cm high, tunics brown, membranous, the outer of minute parallel fibers, forming basal rhizomes. Rhizomes solid, jointed, sometimes branching, 4–20 cm long, with sheaths 5–6 mm long, withering, terminating in a cormel at dormancy. Leaves 3–4 (7), 2–4 mm in diameter, to 50 cm long, erect, scabridiusculus, with minutely crenulated nerves, terete to subterete, glaucescent dark blue-green, flattened adaxially, rounded abaxially, becoming prostrate at anthesis; scape 30–55 cm tall, smooth, 2–5 mm diameter, glaucescent light green. Spathe bracts 3–7, deltoid, 1–2 cm long, withered at anthesis. Umbel 2 (3–7) 11 flowered, pedicels articulated with perianth tube, 1–10 cm long, unequal, the outermost generally the shortest. Flowers nocturnal, fragrant, perianth tube with lacunae between flanges of the gynophore to the base, 12–18 cm long, 2 mm wide at base, greenish, 4–5 mm wide at ventricose green-and-white throat, flushed purplish; segments 2.5–3 cm long, outer segments 7–8 mm wide, inner segments 8–9 mm wide, elliptic, white abaxially, with 7-nerved green stripes, flushed purplish-brown

adaxially; filaments as long as anthers, exserted 1.5–4 mm, subulate, smooth, white; anthers bluish or greenish, 4 mm long, pollen whitish; ovary 1–1.2 cm long, on a gynophore 11–17 cm long; style 1.5 cm long, longer than the stamens, stigma papillate at margins, smooth at center; capsule 2–2.4 cm. long, 7–10 mm wide, ellipsoid; seeds wrinkled, black, shining. $2n = 54$ (fide Lenz. 1971).

Distribution: Mexico, state of Puebla, south of Tehuacan, and vicinity of Izucar de Matamoros, in semi-arid regions in south-central and southwestern sections in chalky soils and outcroppings. Also in adjacent states of Morelos and central Guerrero, flowering September–October.

Milla mexicana is a late summer or autumn flowering nocturnal species having narrowly terete, scabrous dark green leaves, forming slender, elongate horizontal, scaly rhizomes, sometimes branching, terminating in a small cormel after anthesis. The flowers are fragrant with an anise-like scent, one or two opening each evening and closing before dawn. Thus they are unnoticed during daylight hours, and probably have been confused with *M. biflora*, which accounts for the nocturnal species being unknown to science (the flowers of *M. biflora*, *M. rosea*, *M. bryanii*, and *M. filifolia* remain open both night and day). *Milla mexicana* is nearest morphologically to *M. magnifica*, *M. potosina* and *M. oaxacana*. It differs from *M. magnifica* in being more slender with narrower scabrous leaves, smaller corms and fewer, smaller flowers, though it may be as tall. As with *M. magnifica*, foliage is erect until anthesis, but sprawls afterward. From M. *potosina* and *M. oaxacana* it differs in being taller and more robust, with erect, terete foliage, taller scapes, articulated pedicels, seven-nerved keels, and formation of slender scaly rhizomes that form new corms at their apices. The chromosome number is $2n = 54$, the highest known number reported in the genus (Lenz, 1971).

Milla potosina T.M. Howard sp. nov. (Fig. 2)
Cormus 1.5–2 cm diam. 1.5–2 cm altus; folia 4–8, gramini, 25 cm longa 1.5–2 mm lata: scapus 10.6–20 cm altus, 1.5–2.5 mm diam., bracteis 1–1.5 cm longis, umbellam 1.6 floratam gerens; tepala trinervata, elliptica, nocte patens; stamina exserta filamentis 1–2 mm longis, antheris 5 mm. longis.

TYPE: *Howard 67–84* (holotype: MO).

Corm solitary, 1.5–2 cm diameter, with collar, 1.5–2 cm high, with membranous brown tunics, forming basally attached cormels with age. Leaves 4–8, narrowly linear, grass-like, concavo–convex, 1.5–2 mm wide, ca. 25 cm. long, smooth, or with minute hyaline-denticulate nerves, glaucescent. Scape 10.6–20 cm tall, 1.5–2.5 mm diameter at base, smooth, glaucescent; spathe

bracts 1–1.5 cm long, withering at anthesis. Umbel 1–6 flowered, sessile, or with unequal indistinct pedicels. Flowers1–2.5 cm long, fragrant, nocturnal, remaining closed during the day, perianth tube greenish with green stripes, 6–14 cm. long, with lacunae between the flanges of the gynophore within 5–20 mm of the base, the tube and gynophore fused into a pedicel 1.2 mm wide at base, 5 mm wide at the slightly ventricose throat, segments 2–2.5 cm. long, white with 3-nerved green stripe adaxially, white abaxially, 7–10 mm wide at middle, the outer segments narrowing slightly at base, margins flushed purplish, the inner segments distinctly narrowed to a short claw at base, overlapping; filaments subulate, exserted, 1–2 mm long, smooth, white; anthers 5 mm long, pollen bluish or whitish; ovary 10–12 mm long on a gynophore 12.5 cm long, style 1.5 cm long, exceeding anthers 5 mm, stigma papillate at margins, smooth at center, capsule ellipsoid, 2 cm high, 7 mm diam., seeds coarsely granular, 5 mm long, 2 mm wide, dull black, wrinkled. $2n = 18$ (fide Lenz 1971).

Distribution: Mexico, states of San Luis Potosi, southeastern Zacatecas and southern Nuevo Leon. Semi-arid. rocky hills and open scrub on level ground with xerophytes in calcareous soils.

Milla potosina is common in the rocky hills around the city of San Luis Potosi. A xerophytic species, it is fragrant and nocturnal in flowering habit, the flowers opening singly in the evening and closing between midnight and dawn. The corms and foliage are nearly indistinguishable with those of *M. biflora*, with which it has often been confused. *Milla potosina* is morphologically allied to *M. oaxacana* of southern Mexico, but the flowers have shorter staminal filaments (2 mm vs. 3 mm in *M. oaxacana*), a chromosome number of $2n = 18$ (instead of $2n = 16$), and the keels have three nerves instead of five. Also, the populations are geographically remote from one another by five to six hundred miles of mountains and valleys to the southeast.

Milla filifolia T.M. Howard sp. nov. (Fig. 3).

Cormus 1–1.5 cm diam.; folia 4–8, gramini 20–26 cm longa, 1 mm lata; scapus 10–23 cm altus 1 mm diam. Puberulus, parte inferiore quint purpurea, bracteis 6–9 mm longis, umbellam 1–6 floratam gerens; flores pedicellis 10–30 mm longis, puberulis, tubis 4–7 cm longis ad basin 1 mm diam. ad faucem 5–6 mm diam. gradatim dilatis; segmentis patentibus 1.5–2.5 cm longis; stamina exserta filamentis 1 mm longis, antheris 2–6 mm longis; ovarium 5–8 mm longum stipite 5.5–12 mm longo. Typus: *Howard 64–79*, MO.

Corm solitary, about 1–1.5 cm diameter, about 1 cm high, with membranous brown coats, producing basal cormels; leaves 4–6, 20–26 cm long, 1

mm wide, subterete, filiform, minutely channeled adaxially, convex abaxially, lax, sprawling, light green; scape 10–23 cm tall, 1–1.5 mm diameter, wiry, minutely pubescent with closely set bristles about .5 mm long, purple in lower fifth; spathe bracts 67–69 mm long, withering at anthesis. Umbel 1–6 flowered; pedicels 10–30 mm long, unequal, minutely pubescent; articulations not always distinct. Flowers white with green stripes, sometimes flushed purplish abaxially, on, fragrant, opening at noon, remaining open for several days and nights; perianth tube 4–7 cm long, with lacunae between flanges of the gynophore to the base, 2 mm wide at the base, 3 mm wide at the more or less constricted throat, segments 1.5–2.5 cm long, outer segments elliptic, 6 mm wide, inner segments 8 mm wide; white on upper surface, with 3 green nerves on lower surfaces; filaments subulate, white, smooth, shorter than anthers, 1 mm long, anthers subsessile, 2–6 mm long, pollen yellowish; ovary 5–8 mm long, on a gynophore, 5.5–12 mm long, style longer than anthers, capitate. Capsule ellipsoid, 13 mm long, 8 mm wide; seeds numerous, dull black, coarsely granulated, wrinkled. $2n = 18$ (fide Lenz, 1971).

Distribution: Mexico, Morelos, east of Cuernavaca, near Yautepec and Cuautla, on Mexico 11 S. Also southern state of Mexico, near Guerrero border, Mexico 55, in volcanic hillsides in short grasses, ca. 5250 feet altitude.

Milla filifolia ocurs in the same geographic area as *M. biflora* but populations do not occur together. It differs from that species in having smaller corms, thread-like leaves, minutely pubescent pedicels and scapes always purplish at the base. Like *M. biflora*, the flowers remain open for several successive days. The flowers are easily differentiated from *M. biflora* as the filaments are

Fig. 1. *Milla mexicana.* Photo by T. M. Howard.

Fig. 2. *Milla potosina.* Photo by J. Chris Pires.

Fig. 3. *Milla filifolia*. Photo by T. M. Howard.

longer and the pedicels are well articulated. *Milla biflora* is taller and more robust in habit, and generally has smooth shiny stems, within their range. By comparison, foliage of *M. filifolia* is unusual in that the leaf width is a constant 1 mm, regardless of the corm size and age, while leaves of *M. biflora* vary in width with the age and size of the corm. It is the same situation with the corms: those of *M. filifolia* usually do not exceed 1.5 cm diameter, while those of *M. biflora* are larger, varying according to maturity and culture. The wiry, purplish, pubescent scapes make *M. filifolia* easy to determine from other *Milla* species. Stamen filaments of *M. filifolia* are about 1 mm long, while those of *M. biflora* are sessile. The keels (nerves) on the underside of the perianth segments of *M filifolia* differ in being relatively wider, and colored a soft olive-bluish-green and may be flushed purplish in varying intensity, but this characteristic is not useful in determining one white-flowered species from another.

Lenz (1971) determined the chromosome count of *M. filifolia* as $2n = 18$, whereas the chromosome number for *M. biflora* is mostly $2n = 42$ (43). Other collections of *M. biflora* from central Mexico were $2n = 14$. According to Lenz (1971), there is a polyploid series within the wide distribution of *M. biflora* based on $x = 7$ including diploids, tetraploids and hexaploids. Lenz (1971) also reported that two collections of *M. biflora* appear to be based on the haploid number of eight, one of them diploid with $2n = 16$ and the second possible hexaploid with $2n = 48$.

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BOOK REVIEWS

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Good horticultural books, each contributing to our appreciation and knowledge of a genus or grouping of plants, seem to flow like a never-ending stream from Timber Press of Portland Oregon. We may consider ourselves to be well informed and knowledgeable, but I have yet to read a book from Timber Press that has not expanded my knowledge.

This grand publishing firm (we owe Richard Abel a big thank you for his efforts in getting this firm underway) has the knack of attracting the most knowledgeable of authors. I would submit their "Gardener's Guide" series as valuable and comprehensive examples. Various genera are discussed in each, and the books are perfect for acknowledged experts in one area who wish to lay a solid foundation for knowledge in another. The price is also right at $29.95. Two such books are **The Gardener's Guide to Growing Fritillaries**, by Kevin Pratt and Michael Jefferson-Brown, and **The Gardener's Guide to Growing Daylilies**, by Diana Grenfel.

The Gardener's Guide to Growing Daylilies, by Diana Grenfel. Timber Press, Portland OR. $29.95. ISBN: 088192461X

Asked by the Hardy Plant Society to form a *Hemerocallis* Study Group, Diana Grenfel was so enraptured by the genus she went on to contact growers around the world, and soon formed the British *Hosta* and *Hemerocallis* Society. She is a co-founder, first Chairman and now Vice-President of this society.

I had not appreciated there are over 40,000 cultivars of *Hemerocallis* registered. But I have noticed an ever-increasing number of daylilies being used in major landscape projects. Is this surprising? I think not, especially after reading daylilies are featured in paintings and folk legends dating back to Confucius (551–479 BC) While ancient, they have not escaped the attention of recent molecular DNA studies. Such show these plants are most closely related to *Phormium* which would place them in Phormiaceae.

Such information I find both fascinating and disturbing. Are we going to be obliged to accept completely different criteria in identification and classification of some of our favorite plants? I would have liked to have read the author's comments on such; after all, being an acknowledged expert, her opinion would no doubt provide much food for thought.

However, there is much to appreciate, and the chapter "Modern Hybrids and Their Terminology" is interesting, even if we do have to wonder at such headings as "Macrodefintions" and "Microdefinitions". Discussing the height

of scapes, the author states "*such is more subject to climatic and soil variation than the size of the blooms*" and goes on to say, "*Daylilies raised in Florida and the Deep South of America often have lowish scapes, due to the selection by breeders of lower and lower scapes and the intensity of the sun. In certain daylilies the length of the scape is such that the flowers are held among the leaves or only just above them. Such does not seem a good trend*". The author goes on to say, "*For garden use it is much more desirable to have scapes that are tall enough to hold the flowers well clear of the foliage, and much has been done to ensure that this is now the norm*".

Upon reading this, one can not but wonder why such cultivars were ever introduced. Is this proclivity of the author to state such things, and leave the subject "dangling," a way to make the reader think for himself? Is this an advantage or a disadvantage? How interesting to read personal comments of the author on such things, but, because of her love and knowledge of these plants, I would like her to have expounded a little more. More would have been much better, in my opinion.

The descriptions of the species, the chapters on "Selection of the Best Daylilies", "Cultivation", and the other subjects covered, make this a book that many will appreciate, and one that all gardeners should consider for their libraries. Sound, sometimes provocative, text, and over 70 great full-color photographs make this is a good book to have.

The Gardener's Guide to Growing Fritillaries, by Kevin Pratt and Michael Jefferson-Brown. Timber Press, Portland, OR. $29.95. ISBN: 0881923877

When the extensive horticultural knowledge of Jefferson-Brown is coupled with Kevin Pratt's equally extensive understanding of the genus (he is the holder of the National Collection of Fritillaries which contains over 100 species), you have a combination of talents which just can not miss, and did not.

The photography in this book is superb (over 90 color plates), and with the 13 line drawings they combine to present to the reader a comprehensive "micromonograph" (borrowing a phrase from **Daylilies**) which all interested in growing these fine plants should read, mark, learn from, and inwardly digest. It will not cause indigestion but provide hours of pleasant reading.

While reading is "pleasant", I feel the description of the fragrance of *Fritillaria imperialis* as being "foxy" is mild, to say the least. I once heard it described as smelling like "rotting mutton" and I think this is closer to the mark, but would such a description sell these plants? Perhaps the authors are here being "foxy" themselves. I looked in vain for an explanation of the double ring of flowers I observed on this species growing in one of the royal gardens in the Netherlands. A pity.

Describing *F. bithynica*, the authors state : "*This is a confusing species with numerous variations, some with recognized names, but only slightly different from the type plant*". He then presents the illustrations of *F. bithynica*, *F. b. carica*, and *F. b. c. serpenticola*, which makes one appreciate the authors comment about being a confusing species! The descriptions of the species are well written, and the provision of their habitats is so useful, that this is truly a great guide for gardeners growing any of the species.

I do not remember seeing a chapter with the title of "Buying and Cultivating" before, but there is one in this book. "Breeding and Propagation", "Plant Associations", all such chapters contribute to our knowledge of this attractive genus.

The Cape Floral Kingdom by Colin Paterson-Jones. New Holland, Capetown. ISBN: 1853684813.

It is hard to imagine a richer flora than the Cape Floral Kingdom of South Africa. In a book with that title, Colin Paterson-Jones has assembled a collection of photographs which does justice to this botanical magnificence. Published by New Holland Publishers Ltd., 24 Nutford Place, London W1H 6DQ, the book brings to our attention the natural magnificence of the Cape.

Occupying only a fraction of a per cent of the world's land area, the Cape enjoys equal status with all of North America, containing some 950 genera and over 8,500 species that are endemic. It behooves all who love plants to acknowledge the importance of the region. This book will be of great assistance in achieving this.

In my opinion (and I am sure the opinion of many), plants that are companion plants in the wild for many of our beloved bulbs should be appreciated. Will future developments in the field of symbiotic relationships establish the importance of plants found growing in association with each other? I think the jury is still out on this. A subject of some future study perhaps?

The bulbs shown in this colorful work give insight on how our favorites look in their native habitat. *Cyrtanthus, Haemanthus, Sparaxis , Brunsvigia, Romulea, Babiana, Hessea, Gladiolus, Ornithogalum, Gethyllis, Watsonia, Lachenalia and Moraea* (often several species of these genera) are depicted in glowing and glorious color.

Brief but accurate descriptions of the localities where the plants are at home are given. Such information is invaluable for growers to know. Seeing the photograph of *Pillansia* with *Watsonia borbonica* subsp. *borbonica*, will make you appreciate the beauty of these plants, and indelibly imprint on the mind the flowering time they share. You will see the rocky areas where *Freesia alba* grows, and how *Cyrtanthus elatus* establishes itself in communi-

ries. You will, without a doubt, wish to head to the Cape in the year 2000 for the ISHS Flower Bulb Symposium and perhaps join me afterwards for a tour of the Cape's floral bounty.

Corydalis—A Gardeners Guide by Magnus Liden and Henrik Zetterlund. Alpine Garden Society. £24.00.

The Alpine Garden Society has published an excellent book, **Corydalis, a gardener's guide and a monograph of the tuberous species**. Magnus Liden & Henrik Zetterlund are the authors, the editor Christopher Grey-Wilson. In the acknowledgments credit is given to Brian Mathew, for inspiration, information and for triggering the world-wide *Corydalis* craze in 1981. Has Brian ever been associated with a poor or sub-standard book? Not to my knowledge.

This is without a doubt a scholarly work. What is a *Corydalis*? This question is posed and answered. Basically *Corydalis* embraces species with a zygomorphic corolla, a persistent style and a racemose inflorescence. Why *Ceratocapnos claviculata* is more closely related to *Fumaria* and can not be retained in *Corydalis* and why *Corydalis lutea* is separated out as *Pseudofumaria lutea* is explained. Can you doubt the quality of the scholarship?

There is a "Historical Resume" given, and a brief chapter on "Vernacular Names". The "History of Cultivation" is based on British literature, and it is noted this may cause it to be rather insular in coverage. I hope you would not expect me to agree with that!

An interesting, albeit short, chapter is "Pests in Nature". "Pests and Diseases in Cultivation" is twice as long; it makes one wonder what man has wrought. "The Tuberous Species" are discussed in detail, and the key to species of section *Corydalis*, must be a little unusual as it is divided into geographic species groups. If one does not know a species' geographic origin, it becomes difficult to determine its identity. However, the "Key to the Tuberous Sections" is short and to the point, so one is soon on the right track. I often wonder just how true are classifications by size; can the difference of 1 mm make a difference? Couldn't soil and climate possibly wreck havoc with such distinctions? The Horticultural Divisions recognized are also a little unusual, titled The Western Woodlanders, The Bulb-Belt Species and the Eastern Woodlanders.

The photographs in great color and the line drawings will prove to be invaluable for identification of the species. There is no sparing of detail and combinations of characteristics given. Do you know where Novosibirsk, Altai, Tomsk Kuznetsky and Alatau are? Fortunately, you are referred to Map 9; unfortunately these maps (and there are some 36 of them) are rather small and sometimes difficult to place when no familiar land-mass can be spotted.

There is much that is great in this book. Comments such as "*a superb species that remains compact in cultivation*" referring to *Corydalis macrocentra*, are invaluable and of great help to those wishing to select species to grow in their collection. On the other hand, who would be tempted by one described as "*a rather inconspicuous species of limited horticultural value*". It is refreshing to read such comments, and such information is invaluable. Without a doubt, if interested in *Corydalis*, you must have this work.

Summer Bulbs: Simple Steps for Growing Beautiful Glads, Dahlias, Begonias, Cannas, and Other Tender Bulbs by Henry Jaworski. Houghton Mifflin. $20.00. Paperback. ISBN: 0395892619.

All too frequently, those not intimately concerned with bulbs associate them with spring, forgetting the summer flowering bulbs that can add so much pleasure to our summer gardens. This rather unpretentious book will help correct the false impression that bulbs only flower in the spring. It is well worth the price of $20.00.

I wonder if *Ferraria crispa* will ever be commonly grown in our gardens? Let us hope so; the photograph in this book shows this species to advantage (I confess it is one of mine!). There are other very good photographs in the book, which might well be just the one to turn some people on to bulbs.

An interesting section deals with "How to Import Bulbs". I suppose this subject must have been mentioned in other books, but I can not recall them as I write. I would not agree with the author when he says that Ogier Ghislain de Busbeq smuggled a few bulbs to the Imperial collection in Vienna from his posting as Ambassador to the Ottoman Empire. After all, he was sent to sue for peace! Nor would I agree that Clusius stole the entire Imperial collection when he accepted the post of botany professor in Holland. Rewriting of history is apparently also to be found in horticulture. A pity this, as the true story is just as romantic, if not more so.

Altering common names, such as Nile Lily, instead of Lily of the Nile, with no mention of its other common name, Harriet's Flower, for *Agapanthus*, is a little annoying, but I was pleased to see such lesser known bulbs as *Bessera*, *Sandersonia*, *Scadoxus* and *Littonia* displayed in full color. It is about time more people knew of these beauties. However, I do wish people would appreciate that Kaffir lily is a derogatory name and stop using it.

This book has a few other problems. Exact height and time of flowering are examples of information that is sometimes missing. Would you consider *Clivia miniata* to be a summer flowering bulb? Mine flower from November to April, but then I live in San Francisco. Such details should have been

included. This book does give an indication of just how many fine bulbs will give us summer color and I wish more books did so.

The Genus Arum by Peter Boyce. Royal Botanic Gardens, Kew. $50.00. Paperback. ISBN: 0112500854

This Kew Magazine monograph is obviously a must for all aficionados of this genus. The author, Peter Boyce, is a botanist at the RBG Kew, unusual perhaps as he believes examining living material is an important aspect of taxonomy. Would that more botanists were also of this persuasion.

The genus is one where the structure of the tuber is of fundamental importance for accurate identification of species. There are two types, horizontal-rhizomatous and discoid. Types of roots, comparison of flowering modes, morphology of inflorescences, leaves and petiole-sheath are, in a most interesting way, discussed, and well-illustrated by drawings.

Did you know (or want to know?) that the species *A. maculatum* and *A. italicum* contain tiny amounts of an alkaloid similar to conine, the active poison in Hemlock (*Conium maculatum*)? Or that recent doubt has been cast on this? I find such details about plants makes for more interesting reading.

Here is what the author says regarding one aspect of pollination. "*Soon after sunrise the spathe unfurls and insects begin to gather in the vicinity, attracted by the strong dung-like smell of the spadix appendix. The prospective pollinators land on the outside of the spathe-limb, and walk onto the inner surface. Here they are unable to maintain a grip on the oily surface, their struggles simply releasing more oil from the epidermal cells, and eventually they fall into the spathe-tube. Once trapped, escape by climbing out is prevented by the oily spathe-wall, and by the oily surface of the spadix above the pistillate flowers*". Fascinating stuff this. I can almost imagine the insects lining up and taking a number! George Lucas, does this inspire you?

Taxonomy is discussed in depth, keys to the subgenera (*Arum* and *Gymnomesium*) and to the sections and subsections as well as a species and subspecies, are well presented. The illustrations are superb colored drawings, and good-sized maps are included to show the distribution of the species. The line drawings are wonderfully done, and the descriptions are humane, not simply cut and dry.

The genus *Arum* might not be a favorite of yours, but this book will intrigue you because of the way the information is presented. Monograph writers should study the way the book is presented. Without a doubt, it will increase your appreciation of the genus *Arum*. The author deserves a good pat on the back and congratulations on a job well done.

HERBERTIA 54 — 1999

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Compiled by Alan W. Meerow

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5. Descriptions of taxa must follow conventional form as to construction of descriptive paragraphs, specimen citation, and synonomy. Use the following example as a guide or consult journals such as *Systematic Botany*, *Brittonia*, or *Annals of the Missouri Botanical Garden*:

Eucrosia aurantiaca (Baker) Pax. Die Nat. Pflanzenfam. (A. Engler and K. Prantl, eds.), 15a: 415 (1930).

Callipsyche aurantiaca Baker. Refug. Bot. 3:t. 167 (1869). Neotype: Ecuador, El Oro, Ayabamba, 200 m, Andre 4262 (K).

Eucrosia morleyana Rose. Addisonia 7: 3-4, pl. 226 (1922). Type: Ecuador, Chimborazo, Huigra, 4000 ft, Rose & Rose 22593 (holotype, US; isotypes, GH, NY, S).

Eucrosia eucrosioides var. *rauhiana* (Traub) Traub. Pl. Life 22: 62 (1966). *Callipsyche eucrosioides* var. *rauhiana* Traub. Pl. Life 13: 61 (1957). Type: Ecuador, Azuay, Pasaje, 300 m, Rauh & Hirsch E15 (holotype, MO)

Bulb large, 7.7–10 cm long, 6–7.7 cm in diam.; tunics tan-brown; neck (2.5)5–8 cm long, 2–2.6 cm thick. Leaves 2, hysteranthous; petiole 27–35 cm long, 7.5–10 mm thick, deeply channelled for most of its length; lamina ovate-elliptic,

29–40 (50) cm long, (12) 16–22 (29) cm wide, acute or short-acuminate, basally attenuate to the petiole, thick, coarsely undulate, hypostomatic, abaxial cuticle thickly striate and non-glaucous. Scape (5) 7–9(10) dm tall, ca. 10 mm in diam. proximally, ca. 4–6 mm in diam. distally; bracts 3(5) cm long, lanceolate. Flowers (7) 10–12 (13), zygomorphic, all reaching anthesis concurrently, more or less perpendicular to the axis of the scape; pedicels (11) 22–33 mm long, 1–2 mm in diam.; perianth (2.8) 3–4 (4.4) cm long, green in bud, yellow at anthesis, rarely orange or pink, compressed laterally giving the perianth a somewhat flattened appearance; tube sub-cylindrical, 5–7 mm long, ca. 5–6 mm wide, constricted at the ovary to ca. 3.8 mm wide, concolorous with the tepals for for most of its length, green only at the base; tepals spreading dorsally and ventrally to 23–29 mm wide, recurved and sometimes stained green apically; outer tepals (20) 23–29 (36) mm long, 5–6 mm wide, apiculate, lanceolate, keeled, 2 of them situated laterally, one dorsally; inner tepals 20–26 (34) mm long, obtuse, oblanceolate-spatulate, margins undulate at the middle, 2 of them ca. 9.5 mm wide and situated laterally above the 2 lateral outer tepals, the third one 5–7 mm wide, ventrally declinate and with the lower lateral tepals forming a pseudo-labellum. Stamens subequal, 8.5–11 cm long, filiform, long-declinate, ascendent in their distal 1/4, green; filaments dilated and connate in their proximal 2–3 mm; globose nectar glands present at the perianth throat, each 1–2 mm in diam.; anthers 5.5–6 mm long, oblong; pollen green, the exine mostly tectate-perforate. Style 10–11 cm long, green; stigma less than 1 mm wide. Ovary ellipsoid, 6.5–9 mm long, 4–4.5 mm wide; ovules 20 or more per locule. Capsule 2.5–3 cm long, 17–22 mm in diam.; pedicel 5–6 cm long; seeds numerous, blackish-brown, ca. 6.5 mm long, 1.5 cm wide. $2n = 46$. Flowering July–September and December–January.

ECUADOR. El Oro: between Santa Rosa and La Chorita, 0–100 m, Hitchcock 21139 (GH, NY, US). Chimborazo: Río Chanchan canyon between Naranjapata and Olimpo, terrestrial in rock wall crevices, 800 m, (ex hort), Horich ISI # 214 (UC). Between Huigra and Naranjapata, 600–1200 m, Hitchcock 20638 (GH, NY, US). Cañar: valley of Río Cañar near Rosario, 960 m, Prieto CP-18 (NY, S). Azuay: Road from Jiron to Pasaje, near Uzhcurrumi, dry, steep, rocky hillside, 840 m, Plowman et al. 4600 (GH), Plowman 7634 (F), Plowman 12024 (F). Km 97 on road from Cuenca to Saraguro, dry thorn scrub, ca. 1100 m [incorrectly typed on specimen label as 2400 m], Madison et al. 7517 (SEL).—Inhabiting semi-desert and dry, rocky canyons and hills of the lower inter-Andean valleys (100) 300–900 (1100) m. Endemic.

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