Odontoglossum Alliance Newsletter

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In this Issue

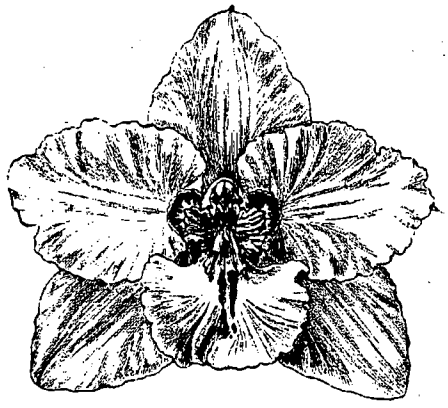
Part 2 of Stig Dalstrom's Article

Part 4 of Helmut Rohrl's Article on Hybridizing

Information and Program for the Odontoglossum Alliance Meeting in Hawaii

Membership Status of the Alliance

Les Odontoglossum by Leon Duval Release



WHEN ONE AND ONE BECOME THREE, AT LEAST

By
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Part two

The intention with my thorough study of *Odontoglossum* is primarily to solve the taxonomic confusion in this particular group of plants. Secondarily, it is also an attempt to find "behavior" patterns, or taxonomic keys, that can be applicable on other groups of plants as well. Two American Orchid Society recognized "experts" have recently published independent treatments of the genus *Cochlioda*. Dalström published in Selbyana, December of 2001, and Christenson published in AOS Orchids, February of 2002. Despite the limited numbers of taxa involved, the treatments are amazingly different. Dalström recognizes four good species (*C. densiflora*, *C. mixtura*, *C. rosea* and *C. vulcanica*) but includes *C. chasei* despite its doubtful authenticity. Christenson recognizes seven species (*C. beyrodtiana*, *C. chasei*, *C. densiflora*, *C. miniata*, *C. noezliana*, *C. rosea*, *C. vulcanica* and one natural hybrid *C.* x *floryi*). A comparative discussion is therefore justified.

The genus *Cochlioda* was described by Lindley in Folia Orchidacea, 1853, based on a plant collected by A. Mathews in Peru about fifteen years earlier. Lindley named it *C. densiflora* in reference to the dense inflorescence. The type specimen (holotype) is in the Lindley herbarium at Kew (K-L). Additional specimens (isotypes) are located at the British Museum in London (BM), and also at the Reichenbach herbarium in Vienna (W). When we analyze the flowers from these specimens we discover certain unique features that when combined create a distinct profile that readily separates *Cochlioda densiflora* from other species. The

most distinguishing features are the colors of the flower and the shape of the column and lip (**slide 10**), which when dried create a very characteristic shape with the column extending way beyond the broad and recurved lamina of the lip. The sepals and petals range in color from a rare yellow through pale brick red, bright orange to deep red. The callus, however, is consistently yellow and the tip of the column is consistently lilac to magenta. The shape and size of the sepals and petals vary considerably too but the shape of the lip and column is quite consistent. In order to understand the natural variation of any species it is essential to study large numbers of plants, preferably in the wild. When this is not possible a convenient shortcut is to visit an orchid nursery with enough wild collected plants in bloom, such as Manuel Arias' greenhouses near Lima, Peru (**slide 11**). In November of 2001, I had the pleasure to visit this orchid heaven and happened to hit the peak of the flowering season of *Cochlioda densiflora*. When viewing hundreds of flowering plants it is easy to get an idea of which characteristics are consistent and specifically important versus which are variable and unimportant, or "cosmetic". This is not to ignore that fact that the variability in itself can be important for other reasons (part in a deceit pollination strategy as an example). Other variable features are the size and shape of the floral bracts and the length of the inflorescence. Among the hundreds of blooming plants in Arias' greenhouse none carried more than one leaf per pseudobulb and only one single branched panicle could be observed. I learned more about this species in one hour than I would have in years of field studies. When we better understand the extent of the natural variability we can also approach the taxonomic confusion, which despite the small size of the genus *Cochlioda* is impressive. Christenson treats *C. densiflora* as distinct from all other species in the genus due to the large and papery bracts on the type specimen. This particular feature is misleading because the size and shape vary, not only between individual plants but also on the same inflorescence. Commonly, larger bracts can be observed basally which then gradually decline in size throughout the length of the spike. A similar habit can be seen in other species, particularly *C. vulcanica* (**slide 12**). The variability of the bracts is not geographically limited (as for a possible sub-specific feature) but varies within the populations and is useless as a distinguishing feature. Christenson also mentions that a generically unusual branched inflorescence is not uncommon for *C. densiflora*, despite the fact that the illustration which accompanied the original description of *Cochlioda noezliana* by Rolfe in Lindenia, 1891 (**slide 13**), displays a plant with widely branched inflorescences. In fact, when available material of what has traditionally been treated as separate species is analyzed and compared no distinguishing features can be found which would support separating *C. densiflora* from *C. noezliana*. Schlechter reached the same conclusion and wrote in The Orchid Review, page 356, 1924: "Some time ago, I discovered in the Herbarium of Reichenbach, fil., in Vienna, not only this much-sought-for tracing of Lindley's type [of *C. densiflora*], but also duplicate material of Matthews' collecting that had evidently been dedicated to Reichenbach by Lindley himself. This material shows quite plainly that *C. noezliana*, Rolfe, is exactly identical with Lindley's *C. densiflora*. As Lindley's name was given to the type plant of the genus, and was published as early as 1853, *C. noezliana* Rolfe, published in 1891, must now be regarded as a synonym of *C. densiflora* Lindl." Christenson declares that it is odd that *C. densiflora* has not been used in hybridization despite the bright coloration of the flowers. In reality, this species is responsible for basically all Odontioda hybrids, but "hiding" behind the name *Cochlioda noezliana*.

Cochlioda miniata (**slide 14**) was described by L. Linden and illustrated in Lindenia, 1896, as a supposed natural hybrid between *C. noezliana* (=*densiflora*) and *C. vulcanica*. The flowers have dark red sepals and petals and a dark orange lip with yellow callus. The column is lilac apically. The colors and shape of the flower, with the column extending beyond the broad and reflexed lip, fall well within the natural variation of *C. densiflora* and nothing can be detected that would support a hybrid origin. Furthermore, the supposed parents have been crossed in cultivation and produce a very different looking flower with white callus, similar to *C. vulcanica*. Consequently, Dalström reduces *C. miniata* into synonymy with *C. densiflora*. Christenson

agrees that *C. miniata* is not a natural hybrid between the supposed parents, but identifies it as a distinct species from Bolivia. This particular species, described as *C. mixtura* by Dalström (**slide 15**), differs from the original *C. miniata* by the color of the callus (whitish versus clear yellow) but primarily in the shape of the lip and column. When pressed and dried, the narrower lip generally stays straight and "hides" the column, which produces a very different outline of the flower. A collection by Miguel Bang near La Paz, Bolivia, represents *C. mixtura* as well, but differs slightly in minor details in the outline of the lip. A feature that is significant enough to be noted on a *possible* subspecific level, but is too similar to the typical *C. mixtura* to be regarded as specifically important. Christenson treats the Bang collection as a separate species and identifies it as *C. beyrodtiana,* which was described by Schlechter, 1918, before he had a chance to examine real type material of *C. densiflora.* Unfortunately, no plant material of *C. beyrodtiana* survived the WW II, but a photograph exists (**slide 16**) which clearly reveals dried flowers with exactly the same shape as for *C. densiflora.* Additionally, all other features in the description, together with the color and origin of the plant (northern Peru) suggest a synonymous treatment.

Cochlioda x *floryi* was described by Rolfe, 1911. He originally thought it was a second plant of *C. miniata* but later changed his mind and assumed it was a hybrid between *C. noezliana* (= *densiflora*) and *C. rosea* (**slide 17**), because the plants had been imported together. Unfortunately, no pressed or illustrated material seems to exist. Nothing in the original description, however, distinguishes it from an inferior form of *C. densiflora*. In fact, the callus is described as yellow which supports a synonymous treatment rather than speculating in a cross between two rather different species which possibly would produce an offspring with a whitish callus (as for the artificial cross between *C densiflora* and *C. vulcanica*).

Christenson and Dalström agree about the identities of *C. rosea* and *C. vulcanica*, which are easily recognized, fairly common and widely distributed species, but disagree totally about the enigmatic *Cochlioda chasei* (**slide 18**), which was described by Bennett and Christenson in Brittonia, 1994. The brief history and identity of this "species" is so contradicting and confusing that it deserves a chapter by itself. Before entering this maze, however, we can draw some conclusions. Plants of *Cochlioda* demonstrate similar distribution patterns as plants of *Odontoglossum*. There are relatively few, widely distributed and variable super-species, which can change their morphology throughout their geographic distribution. This variability has led botanists into misinterpretations and to the description of synonyms.

To be continued...

Editor's Note: This is part two of a three part article by Stig Dalstrom. This material was partially covered by Stig in his lecture at the 2002 Odontoglossum Alliance meeting in Illlinois.

"Les Odontoglossum"

by Leon Duval

Dr. Carl Withner provided the Odontoglossum Alliance with a copy of the book "Les Odontoglossum" by Leon Duval, printed in France in 1900. The Alliance, through the efforts of Dr. Shirley Baker-Thomas, translated the book and the Alliance printed it in a series of newsletters. Now the Alliance is assembling the complete book with both the original French and the English translation. Thanks to the help of Marcel Lecoufle of the French Orchid Society we also have some interesting biographical material. Your editor, Dr. Thomas, Dr Withner and Marcel have been working diligently to have copies available at the Odontoglossum Alliance meeting in Hawaii, 21 March 2003.

Odontoglossum Alliance Meeting

The annual meeting of the Odontoglossum Alliance will be held on 21 March 2003 in Hilo, Hawaii. This is conjunction with the Hilo Orchid Society's 51st Annual Show and AOS Trustees meeting 19-23 March 2003. The Alliance meeting will be held in the afternoon of 21 March and the program is listed below.

Odontoglossum Alliance Program
1:00 PM 21 March 2003
Naniloa Resort Hotel
Hilo, Hawaii

Program Chairperson: James McCully

1:15 PM –2:00 PM
Dr. Helmut Rohrl
Title: **ODONTOGLOSSUM INTERGENERICS**

Many Odontoglossum intergenerics crosses tend to be temperature tolerant. They are usually easy to grow and often have fairly long, branched spikes with many colorful flowers. The flowers are often long lasting and hold well as cut flowers. This talk will be on the hybridizing program and illustrated with results.

Helmut Rohrl started growing and hybridizing Odontoglossums and their intergenerics about 25 years ago. By now he has made close to 7000 (attempted) Oncidiinae and has registered over 200 Oncidiinae crosses. Much of the hybridizing knowledge came from contacts with George Black, Robert Dugger, and Goodale Moir and from material in the Orchid Review and other journals from 1900 to the present. The main goals of the hybridizing effort are: temperature tolerance; vigorous growth; floriferousness; good color and patterns, fairly long, branched inflorescences.

2:00 PM –2:45 PM
Dr. Steven Beckendorf
Title: **ODONTOGLOSSUMS IN VENEZUELA: IS THERE A THERE THERE?**

In both 2000 and 2001 Steve went to Venezuela to seek some of the more elusive Odontoglossum species. This talk will report on what was found, a vibrant culture, friendly people and lots of wild orchids, including several Odontoglossums. Steve will talk some about the species that may still be lurking in the mountains.

Steve Beckendorf started growing orchids about 25 years ago and quickly became fascinated by Odontoglossums and their close relatives because of their variety and beauty, because excellent plants were available from growers and hybridizers on the West Coast, and because of their glamorous past as the most sought after plants in the orchid frenzy that gripped Europe in the 19th century. He soon realized that few of the Odontoglossums species were readily available. He began collecting them for propagation and use in hybridizing. In his attempts to find unusual or lost species he has led several trips to the cloud forests of Mexico and South America. He currently grows about 50 Odontoglossum species and another 30-40 of their near relatives along with many Odont hybrids and a smattering of other cool growing genera

2:45 PM – 3:15 PM **Break. Soft Drinks, coffee and cookies**

3:15 PM – 4:00 PM
James Rassmann
Title: **ORCHIDS IN COLOMBIA AND ECUADOR**

Jim chronicles several trips made recently to Colombia and Ecuador to judge shows and photograph orchids in the wild. Exhibitors were enthusiastic and took the time and effort to prepare exceptional displays showcasing many Andean species not often seen outside their native countries. Many unique clones of extraordinary beauty were seen and often awarded. These trips also offered the opportunity for side travel to forest reserves and private fincas with exceptional and extensive collections.

Jose Vasquez, the older brother of Amando Vasquez, owner of Zuma Canyon Orchids, introduced Jim Rassmann to orchids in 1973. Jose set the hook firmly and Jim has not been able to get free since. Early association with Don Herman via the Orchid Society of Southern California instilled an interest in Cattleyas and he grew a large hybrid collection for nearly twenty yeas in Los Angles. After retiring and moving to the Oregon coast the opportunity to concentrate on cool growing genera presented itself and he now grows primarily Odontoglossums, and a lesser number of Masdevallias, Draculas, Lycastes, Pleurothalids and Miltoniopsis.

Jim has served as President of the Orchid Society of Southern California, American Orchid Society trustee, Vice President and Chair of the Judging Committee.

4:00 PM – 4:45 PM
Andrew Easton
Title: **WHITHER THE ODONTOGLOSSUM ALLIANCE**

Do growers need to defend the "faith", succumb to commercial pressures or try to make a hybrid approach to the often-conflicting requirements of two very different areas of interest?

Andy Easton has been a professional orchid grower since graduating from Colorado State University in 1972. He was introduced to the Alliance by the late Martin Orenstein and Howard Liebman in the late 1970's when he ran Featherhill Exotic Plants in Santa Barbara. He acquired quality plants from Dr. Orenstein's collection prior to his death and these combined with plants from Keith Andrew and Dr. Howard Liebman provided the nucleus of a breeding program at Geyserland Orchids in New Zealand from the 1980's. By 1990 Geyserland Orchids was a major supplier of new Odontoglossum Alliance varieties to Floricultura in Holland and Mukoyama Orchids in Japan. Andy came to the American Orchid Society as Director of Education and Orchid Operations in mid 2000.

Odontoglossum Alliance Dinner and Auction

The Odontoglossum Alliance dinner will be held at the Hilo Yacht Club in Hilo. Cocktails at a cash bar are from 6:00 PM to 7:00 PM and dinner follows. The cost of the dinner is $30.00 per person and includes the dinner and tip. Cocktails are available from the cash bar. Reservations and payment for the dinner may be made with your registration for the Show and Conference.

Following dinner will be a very short business meeting followed by our auction of fine OdontoglossumAlliance material. Included with this auction will be two six packs of the wine glasses from the16th World Orchid Conference in Vancouver. These glasses are monogrammed with The Odontoglossum

Alliance and the 16th WOC. There will be three fine watercolors of Odontoglossums, at least one of which was done by Nellie Roberts in her 50 years of painting the award plants of the RHS. There will also be a significant number of fine plants, seedlings and flasks.

Also available at the dinner will the complete reprint of the book printed in 1900 – **"Les Odontoglossum"** by Léon Duval. This re-printing has been done by your Alliance. It includes the original French material as copied in its original form, a complete English translation, forwards by Marcel Lecoufle and Carl Withner and some interesting biographical material on Duval. This book will be offered by our Alliance for sale at the show and dinner. It will later be available through the American Orchid Society bookstore.

This will be an interesting and informative set of lectures followed by a fun dinner and auction. Hawaii is a great place to visit. There are many orchid nurseries in the vicinity and they will be represented at the sales area of the show.

The conference hotel, The Hawaii Naniloa resort has a splendid location overlooking Hilo Bay, and is just over a mile to the show location. They have obtained a special block of rooms at a discounted room rate of $65.00 standard/superior (plus tax) per night and the rate is available for three days before and after the meetings as well. Please note this room rate can be guaranteed until 30 days prior to the event. A form will be sent with the registration material to be used for making reservations. **(The Odontoglossum Alliance members will be mailed registration material).** A 'room and car' package is also offered through the hotel. The car can be claimed at either Hilo or Kona Airport with return to the same location. Parking is free at the hotel. There will be transportation between the hotel and the Show. Most registrants will want the use of a car to facilitate their activities.

Hilo International Airport is approximately three miles from the hotel and has no direct scheduled air service except inter island within Hawaii. The taxi to the hotel is about $7.00. **Kona International Air Port,** 95 miles east in the leeward side of Hawaii, has good frequencies from California via United, plus numerous flights to Honolulu with connections on Aloha. United is the "Official carrier" to Hawaii. Ask for the **'Orchids in Paradise'** rate UT 500 WI which offers 'zone fares' or 15% off your best fare until January 18. After that, the discount is 10% off best fare until 18 February. Phone 1-800-521-4041.

There is a special rate at the **Outrigger Waikoloa Resort,** valid five days before and after the conference at $145.00 per night plus tax. The Waikoloa can be called at 1-800-922-5533. Ask for the Orchids in Paradise special. The Outrigger is about 22 miles north of Kailua-Kona and is a neighbor of the Hilton Waikoloa. Call for Kona hotels. Hilo is in the Tropic zone. In March, day-night temperatures are mild: 78 to 65. We suggest a windbreaker as it can be chilly on the volcano, and bring a small umbrella for those passing daytime showers. Neckties are optional, and not often seen on the island.

Bringing Plants to the Auction

Bringing plants into Hawaii is like bringing them in from a foreign country. You need an import permit and an agricultural inspection. Taking them out is a similar process. Through the generosity of Jim McCully and Glen Barfield they have simplified the process and made is easy to bring in your plants for the auction and after you buy them, get them home.

To Bring Plants into Hawaii

Send your plants to Steve Beckendorf. He will collect all of them together and arrange with Glen Barfield to have the necessary permits and send them to Glen in Hawaii. Glen will bring them to the Auction and Dinner.

Steven K. Beckendorf
576 Vistamont Avenue
Berkeley, CA 94708

To Bring Your Plant Purchases Home

Glen Barfield will take care of sending your plants to you. He will take care of obtaining the necessary permits and inspections so they can be sent out of Hawaii. He will do this at cost. This is a very generous offer on Glen's part. So taking plants in and out of Hawaii has been simplified and made easy. Whether you are coming to the Meeting and Show or not, please find a few special things and get them to our auction.

Odontoglossum Alliance Dinner and Auction

Through the generosity of Jim McCully our Odontoglossum Alliance dinner will be held at the Hilo Yacht Club. This is about 15 minutes or less from the hotel. Tickets to the dinner are $30.00 per person. The menu is as follows:

Tossed Green Salad
Or
Spinach Salad
Entrée Choice
Shrimp Scampi
Baked or Broiled Fish of the Day
Spencer Roast
Surf and Turf
Rack of Lamb

Rice or Baked Potato
Breads

Special Dessert
Wine with Dinner
Coffee and Tea

Cocktails begin at 6:00 PM with a cash bar. Dinner follows at 7:00 PM. After dinner is the Odontoglossum Alliance auction. Tickets to the dinner can be purchased with your registration material or at the registration desk.

REGISTRATION FOR THE SHOW
INFORMATION PACKAGE
HOTEL RESERVATION FORM
TRANSPORTION

All of this material is available on the WEB at www.hiloorchidsociety.org.
You are strongly urged to use this method for the planning and execution of your trip to Hilo. It is convenient, quick and reliable. It also saves mailing and allows you immediate access to the information need to attend the meeting and show. Please note the dates for registration and hotel reservations to obtain the lowest cost.

Early Show registration Ends on 31 January 2003.

Airline rates escalate after 18 January 2003 and escalate further after 18 February 2003.

Room rates at the Naniloa Resort Hotel can only be obtained for reservations made prior to 30 days before the show.

The Message: Use the Web for information. Register early and make your travel plans in time to take advantage of the discounts.

Membership Status

We currently have 93 paid up members of the Odontoglossum Alliance as of the issuance of this newsletter. In addition we send the newsletters free to 7 people or institutions. These include libraries, the Editor of the New Zealand Odontoglossum Alliance, and other non-profit orchid affiliated institutions. In the year 2001-2002 we lost 10 paying members. In the year 2002-2003 we lost 11 paying members. We have added a few new members. The New Zealand Odontoglossum Alliance is sent to 62 of our paying members.

Dues notices go out with the May issue of the newsletter. Those not paying by August receive the newsletter with a notice that dues not paid by mailing of the November newsletter will be dropped and NO newsletter sent. We permit paying dues two (2) years ahead. It is difficult to get the dues paid on time. Suggestions from our readers would be helpful.

The Monk and the Major

by Dr. Helmut Rohrl
Part IV

Gregor J.Mendel, an Augustine monk in Bruenn, Moravia, studied inheritance of certain characteristics in the garden pea. The concepts of dominance and recessiveness are at the core of his research. He hypothesized that the genetic package of the garden pea contains two versions (what we term ‚alleles') of a particular trait, and that each parent contributed one copy of this trait to every plant in the progeny of a cross. He did, indeed, verify these hypotheses in a series of experiments involving over 300,000 pea plants.

First, he selected individuals of the garden pea with a consistent characteristic (e.g. round seeds), by selfing various cultivars. If the progeny of a cultivar was uniform with respect to that trait, then the zygote matrix of Cross I (species x self) and of Cross V (simple primary hybrid x self) showed that the individual was indeed constant for the trait. If the progeny was not uniform, then the individual was not constant with respect to that trait. Next, he bred a plant A that was constant with respect to a given trait with a plant B that was constant with respect to the alternative trait. He observed that the progeny was uniform in the sense that all individuals of A x B showed the same result relative to the trait (see Cross II). If the trait was the same as that of parent A, then parent A was called *dominant* (and parent B *recessive*) with respect to that trait. From grex A x B he selected two cultivars, cross-bred them, and observed that the new progeny consisted of dominant and recessive individuals at a ratio of 3 : 1. This result is called Mendel's *law of segregation*.

If we denote a dominant trait by |, then an individual constant with respect to this trait has "somatic genome" [||]. For a recessive trait, we use the symbol /, and a plant with this trait has „somatic genome" [//]. Note that a dominant or recessive trait „breeds" according to Cross I and hence should be considered as being "species-like". This interpretation fits the zygote matrix of Cross II: Since | is dominant over /, the progeny of these two individuals has "somatic genome" [|/] whose phenotype (appearance) is that of [||]. Thus Cross V (simple primary hybrid x self) produces Mendel's law of segregation by by noting that the phenotypes of [|/] and [||] are the same. In other words, the law of segregation is a special case of Cross V, where we now look at the phenotype, instead of the genotype.

Another series of Mendel's experiments involved „independent characteristics", defined as follows. Assume we have a characteristic | and its alternative characteristic / (e.g. round seeds vs. wrinkled seeds), and a second characteristic \ and its alternative > (e.g. yellow seeds vs. green seeds). Then | and \ are said to be independent if the hybrid populations [||, \>], [|/, \\ ], and [|/, \>] have the same two characteristics as the population [||, \\ ]. As an example, the characteristics "round seeds" and "yellow seeds" are independent. Mendel found cultivars that were dominant with respect to two independent characteristics, and hence should get somatic genome symbol [||, \\ ]. He also found individuals that were recessive with respect to these two characteristics, and thus are denoted by [//. >>]. As before, the fact that they carried this dominant, as well as recessive, behavior could be checked by selfing them (see Cross I for n = 2). Then he crossed [||, \\ ] with [//, >>] to obtain progeny [|/, \>] (see Cross II for n = 2), all of which showed both characteristics. Then he cross-

bred two individual, one with round and yellow seeds, the other with wrinkled and green seeds, and observed these progeny: yellow and round, yellow and wrinkled, green and round, and green and wrinkled at a ratio of 9:3:3:1. This ratio is referred to as Mendel's *law of independent assortment.* The zygote matrix of the last cross is that of Cross V for n = 2. If we go from the genotypes in the zygote matrix to the corresponding phenotypes, we find precisely this ratio, confirming the law of independent assortment.

Following Gregor Mendel's work, CC. Hurst was the first to conduct scientific studies of inheritance in orchids, beginning in 1896. He studied primarily inheritance of albinism in Cattleyas. He realized that definitive hereditary traits could only be established with pure white forms, not with very pale cultivars (which are usually called albescent forms today). He found that the alba forms, when selfed, always led to alba forms, but when they were bred with normal colored varieties, they produced colored progeny. These latter cultivars, when selfed, resulted in ¼ white progeny and ¾ colored progeny. However, when he bred two different alba forms, results were different. Progeny were either entirely alba forms, or entirely colored cultivars, in which case alba forms appeared in the next generation. Hurst's explanation was that the appearance of color is controlled by two hereditary factors, denoted by C and R. He hypothesized that C and R were dominant for color, and their mutant alternatives c and r were recessive. He reasoned that C was responsible for making colorless chromogen, and R for the presence of an enzyme which converts chromogen into colored pigment. In his view, the recessive characteristic, c, signified the absence of chromogen, and r indicated the absence of the enzyme. This meant that color appeared precisely when a cultivar has both C and R in its genome. As a consequence, [C-, R-] represented the colored forms, while [C -, rr], [cc, R-], and [cc, rr] respresented alba forms, where " – " stood for any of four possibilities of the characteristic or it alternative (C,c,R, or r). The combination Rr is said to be heterozygous for R, while RR is called homozygous for R, and the same for C. The progeny of the cross of two cultivars, both of which are homozygous for one characteristic and homozygous for the alternative of the other characteristic, produced exclusively alba forms, and continued to breed true when siblings were crossed for multiple generations. Hurst's findings are easily checked by setting up the corresponding zygote matrix. Crossing two cultivars, one of which is homozygous for C and homozygous for r while the other is homozygous for c and homozygous for R, leads to completely colored progeny, which is represented by the symbol [Cc, Rr]. Crossing two of these latter cultivars renders the zygote matrix

	[C, R]	[c, R]	[C, r]	[c, r]
[C, R]	**[CC, RR]**	**[Cc, RR]**	**[CC, Rr]**	**[Cc, Rr]**
[c, R]	**[Cc, RR]**	**[cc, RR]**	**[Cc, Rr]**	**[cc, Rr]**
[C, r]	**[Cc, Rr]**	**[Cc, Rr]**	**[CC, rr]**	**[Cc, rr]**
[c, r]	**[Cc, Rr]**	**[cc, Rr]**	**[Cc, rr]**	**[cc, rr]**

Clearly, the ratio of colored phenotypes to alba phenotypes is 9:7; this ratio is called Hurst's *law of prepotency*:

In the cross [Cc, Rr] x [Cc, Rr] the colored forms and the alba forms appear at a ratio of 9:7.

As can be seen from this zygote matrix, it is impossible to determine the progeny when an arbitrary alba cultivar from this cross is used as a parent. This is because the alba forms appearing in the cross have different compositions of hereditary factors regulating the flower color, i.e., different genotypes.

Hurst compiled a list of alba cultivars whose genotype was homozygous with respect to one characteristic and heterozygous with respect to the other characteristic[1]. It must be pointed out that the lists refer *only* to particular cultivars of species and hybrids and that different alba cultivars in the same species or hybrid may have a different composition of the hereditary factors under consideration.

Non-mendelian Inheritance

When the female gamete and the male gamete fuse to form a zygote, the male gamete contributes essentially just the nucleus; nothing else survives in the zygote. The female gamete, on the other hand, contributes a nucleus as well as all other cellular organelles, including mitochondria. Mitochondria, which are the "factories" for producing energy, contain their own unique DNA, and this genetic information from the mother becomes part of the zygote. Inheritance carried by the organelles other than the nucleus is called non-mendelian inheritance. It is a simple concept to grasp, since no exchange of genetic material occurs. However, non-mendelian inheritance in progeny is difficult to assess for two reasons.

Both mendelian and non-mendelian inheritance shape certain traits in the progeny. Non-mendelian traits can be obscured by some mendelian contributions, in particular when those contributions have some degree of dominance.

Plant characteristics affected by non-mendelian inheritance are mostly of a vegetative nature (i.e., vigor, growth habit, floriferousness). Vegetative traits can be evaluated by measurements, flower counts, or qualitative descriptions, such as fullness of a flower or branching habit of an inflorescence. But, unlike flower color, these measurements and descriptions are frequently affected by growing conditions, and tend to change with time. As a result, they are more difficult to attribute to genetic inheritance.

In this context we wish to address the issue of quantifiable inheritance (see [A1], p.581 a.s.o., and [AOS], p.44 a.s.o.). It has long been accepted that certain vegetative characteristics of the progeny of a cross, such as flower size or number of flowers per inflorescence, can be predicted by calculating the *geometric mean* of the parents' characteristics. This geometric mean formula applied to, e.g. flower size, says:

"If pod parent A has flower size 3.0 cm and pollen parent B has flower size 4.0 cm, then the average flower size of flowers from cultivars in cross A x B is the geometric mean of 3.0 and 4.0. This is calculated as the square root of 3 x 4 = 12, which is 3.42 cm."

Applying the geometric mean formula is problematic due to non-mendelian inheritance. The female (pod) parent exerts greater influence on progeny, especially for vegetative traits, than does the male (pollen) parent. The "symmetric" square root of the geometric mean (where 3 x 4 yields the same result as 4 x 3) should be replaces by an "asymmetric" formula such as the cube root of $(x^2)y$. In the above example, when the pod parent has 4.0 cm flowers and the pollen parent 3.0 cm flowers, the expected average flower size of the progeny would be the cube root of $(4^2) \times 3 = 48$, which is about 3.67 cm. However, when the larger-flowered plant is used as the pollen parent, the average flower size of the progeny would expected to be the cube root of $(3^2) \times 4 = 36$, which is about 3.33 cm. Notice the difference in the expected average flower size depending on the pod parent. However, *any* formula proposed for predicting such characteristics in a cross should be applies *only to simple primary hybrids* (species x species) and to the *average of the progeny*, since all other crosses produce a tremendous number of mutually distinct cultivars in the progeny.

Since mitochondria drive certain metabolic reactions, the female (pod) parent in a cross will usually have a considerably greater influence on the metabolism, temperature tolerance, and vigor of the hybrid than the male (pollen) parent does. It is therefore recommended *not* to use as pod parent cultivars lacking vigor, or without the desired temperature tolerance. Since non-mendelian characteristics and their inheritance involve almost exclusively the female parent, they are passed only from pod parent to pod parent, and so on. For instance, to create a line of warm-growing hybrids, then mainly warm-growing plants should be used as pod parents. Also, due to non-mendelian inheritance, a cross and its reciprocal often exhibit marked differences. For this reason, a reciprocal of each cross, where the former pod parent becomes the pollen parent, and vice versa, should be attempted.

The Model and Polyploidy

Finally some comment about the way our model works for polyploid somatic genomes rather than the usual diploid ones. Let us again look at what might be called single *chromosome bundle* genomes. In a diploid somatic cell, the chromosome bundle is normally the chromosome pair. In a triploid somatic cell, the chromosome bundle consists of three chromosomes, and in tetraploids it is built with four chromosomes, etc. Consequently the list of possible gametes, which also includes unreduced gametes, will be larger than the one used in Crosses 1 through 7. For instance, in the case of triploid species, the original list of gametes for the zygote matrix will have to be replaced by

[|] , [||] , [|||],

In other words, we have now 1n-gametes, 2n-gametes, and 3n-gametes; the most frequently occurring ones are the first two. In the case of tetraploid species, the list of gametes becomes

[|] , [||] , [|||] , [||||]

The last symbol, of course, represents the unreduced gamete. Here, the most frequently occurring

gamete is the 2-gamete.

Suppose we look at Cross I, that is, the cross of two triploid cultivars of the same species. In this somewhat more complicated situation the zygote matrix turns out to be

	[|]	[||]	[|||]
[|]	[||]	[|||]	[||||]
[||]	[|||]	[||||]	[|||||]
[|||]	[||||]	[|||||]	[||||||] .

The result is that we still get cultivars of the original species, but now also some cultivars with higher ploidy.

However, in contrast with the previously discussed diploid case, the zygote matrix for triploids does not tell us the probability with which the various cultivars appear, since information about the frequency of appearance of various gametes is missing. As stated previously, gametes of polyploid cultivars mostly have chromosome numbers around half of the polyploid chromosome number. For triploids, almost all gametic chromosome numbers will be 1 or 2. Therefore the cultivars in the zygote matrix that appear with the highest frequency are diploids, triploids and tetraploids. This is very interesting for the following reason. Triploids generally do not produce large and healthy progeny with other ploidy cultivars. But tetraploids crossed with diploids or tetraploids breed successfully. Consequently, fertility of triploids is restored to a certain degree by crossing them with triploids and selecting the resulting diploids and tetraploids in the progeny. These considerations, when applied to triploids, remain valid for the other Crosses II through VII.

To get a feeling for the tetraploid situation, let us consider the model for the cross of a diploid species [||] with a tetraploid simple primary hybrid [//Λ]. Note that there are other tetraploid simple primary hybrids with the same parents, namely [////], [/Λ\ ], [Λ\\ ], and [\\\\ ]. The gametes for [//Λ] are

[/] , [\ ] , [//] , [Λ] , [///] , [/Λ] , [//Λ],

while the gametes for [||] are

[|] , [||],

the last ones in both rows being the unreduced gametes. Hence the zygote matrix is

	[/]	[\ ]	[//]	[Λ]	[///]	[/Λ]	[//Λ]
[|]	[|/]	[|\ ]	[|//]	[|Λ]	[|///]	[|/Λ]	[|//Λ]
[||]	[||/]	[||\ ]	[||//]	[||Λ]	[||///]	[||/Λ]	[||//Λ] .

We leave it to the reader to work out the zygote matrix for the other possibilities arising in Cross I through Cross VII, and the various combinations of diploids, triploids, tetraploids, etc. for all possible gamete genomes, including the unreduced gametes.

By analyzing the resulting zygote matrices the following observations can be made.

The number of mutually distinct genomes in the above zygote matrix is considerably larger than the number of mutual
ly distinct genomes in the original zygote matrix. This remains true for any and all crosses when irregular gametes are taken into account.

Higher polyploidy cultivars will result, although infrequently, from these crosses.

The latter point is interesting, as it invites the conjecture that some contemporary orchid species are actually tetraploids. It could be that a species with 2n = 40 evolved from a species which hundreds of thousands of years ago had 2n = 20 by forming tetraploids, and then the original population of 2n = 20 diploid cultivars died out. If the conjecture is true, then the current species population would actually be 4n = 40. An intriquing question in the context is: why have some rupiculous Laelias 40 chromosomes, while others have 80 chromosomes (see [A2], Appendix)?

Except for the above two points, general interpretations for our model, and the corrections to it, remain unchanged. The conclusions drawn above will continue to be true when unreduced and irregular gametes are considered. Clearly, the model and the conclusions on breeding behavior based on chromosomes remain valid for all *eukaryotes*, that is, cellular life forms other than certain bacteria.

And Finally, the Answer

By understanding the principles of mendelian inheritance, we *can* say how much of a species is in any cultivar of a species or a simple primary hybrid. Even in a complex primary hybrid we have a partial answer: the species parent contributes 50 % to the genome of the hybrid's cultivars. But in any complex hybrid population the situation is much murkier. As we have seen, an incredibly large number of distinct cultivars is possible in model-based progeny. Actual progeny populations are subject to random selection by means of several mechanisms[2]. Regardless of an orchid's floral and vegetative characteristics, it is impossible to make any meaningful statements about the inherited genome of cultivars in a complex hybrid. The phenotype of a complex hybrid plant, including traits such as flower color, size, growth habit, etc., does not generally allow us to know what the actual genotype of the cultivar is. We have seen that phenotypic expressions of a trait from a particular ancestor of a complex cultivar can be *dominated,* or *repressed,* by the genome of other ancestors of the cultivar. Also, a progeny's phenotype can result from the *combination* of hereditary traits from ancestors, creating a new trait that did not exist before. *Polyploidy* surfacing in the progeny can

alter the phenotype of the cultivar in unexpected ways. Finally, the phenomenon of *non-mendelian inheritance,* whereby progeny receives genetic material from one parent only, further complicates the picture.

Summing up these observations, we see the result:

In general, it is impossible to see how much of a species is in a hybrid.

Or to phrase it more poetically:

OH SAY, CAN YOU SEE

MAYBE

Maybe

....

Acknowledgement: Cynthia Hill kindly agreed to read and review this paper. She has made numerous suggestions which led to many improvements of this article. I am indebted to her for the time and the effort she applied to make these pages more readable.

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[SCH] Schlechter, R.: Die Orchideen, 3rd ed. Paul Parey 1992.

[1] Expanded lists can be found in [SCH], p.109, and [W], p. 298 and 300.
[2] See section: The Model and Reality

Editors Note: This is Part IV of the treatise by Dr Helmut Rohrl *"How Much of a Species is in a Hybrid?* The previous parts of the paper were printed in the Odontoglossum Alliance newsletters of February, May and August 2002.

Cochlioda densiflora, Peru (Slide 10)

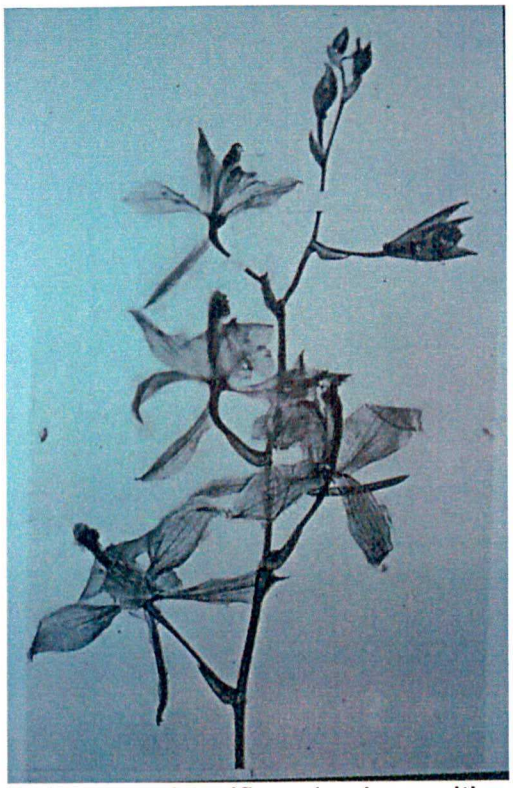
Cochlioda densiflora in Manuel Arias greenhouse, Peru (Slide 11)

Cochlioda vulcnica, Ecuador (Slide 12)

Cochlioda densiflora (as noezliana), illustration of the type (Slide 13)

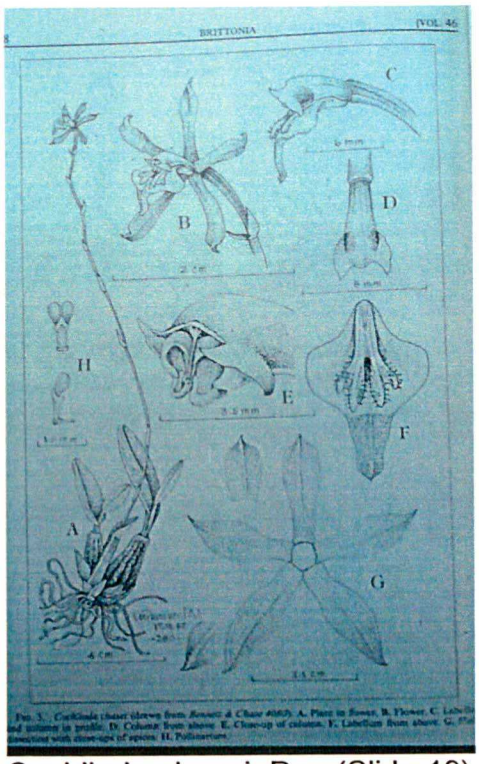
(left) Cochlioda densiflora (as miniata), illustration of the type (Slide 14)

Cochlioda mixtura, Bolivia (Slide 15)



Cochlioda densiflora (as beyrodtiana) illustration of the type (Slide 16)

Cochlioda rosea, Ecuador (Slide 17)



Cochlioda chasei, Peu (Slide 19)