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A Comparative Analysis of Four Populations of *Odontoglossum crispum* Lindl. in Colombia.

Julian Cabal Torrente¹, Ruben P. Sauleda² and Juan G. Saldarriaga³

¹Carrera 71 bis # 125-54, barrio Niza, Bogotá, Cundinamarca, Colombia.
²6442 SW 107 Ct. Miami, Fl, 33173.
³Cra. 5 No 14-05, Casillero 412, Cota, Cundinamarca, Colombia.

Abstract

A comparative analysis of four populations of *Odontoglossum crispum* Lindl. are made. Four plants representing the range of variation found at each locality were chosen for study: Velez, Santander; Cabrera, Fusagasugá, Cundinamarca; Villa Gomez, Pacho, Cundinamarca; San Francisco, Putumayo.

Introduction

Chase *et al.* (2008) state regarding the genus *Odontoglossum* Kunth: "we favor fewer, larger genera ("lumping"), which we believe is easier for users of a system of classification to manage and use. Narrowly circumscribed genera, regardless of how homogenous, result in a system that only specialists can readily and effectively use." Therefore, Chase *et al.* (2008) "lumped" many of the species recognized in the genus *Odontoglossum* into the genus *Oncidium* Sw. Kew (WCSP, 2008) supports this lumping of species of *Odontoglossum* into the genus *Oncidium*.

Odontoglossum crispum Lindl. was transferred to the genus *Oncidium* by Chase *et al.* (2008). The epithet was occupied by *Oncidium crispum* Lodd. The later synonym, *Odontoglossum alexandrae* Bateman was applied to the species. The name accepted by KEW (WCSP, 2008) is *Oncidium alexandrae* (Bateman) Chase & Williams.

We find the comments of Dalström (2012) on this subject relative: "When Chase and others transferred orchid genera *Cochlioda* Lindl., *Odontoglossum* Kunth, *Sigmatostalix* Rchb. f., and *Solenidiopsis* Senghas into *Oncidium* Sw., in Lindleyana (Chase *et al.* 2008), based on molecular evidence (Williams *et al.* 2001a, 2001b, Chase *et al.* 2009), a rather strange situation developed, seen from a taxonomic point of view. Many different looking plants (some mistakenly from the distantly related genus *Cyrtochilum* Kunth) with very different flower morphology, ended up in the same genus. In fact, the flowers are so different from each other that it becomes virtually impossible to visually define the genus *Oncidium*, and to separate it from many other genera in the *Oncidiinae*."

Dalström (2012) adds: "I therefore prefer to treat the visually recognizable species in genera *Cochlioda* Lindl., *Odontoglossum* and *Solenidiopsis* Senghas as a separate and single genus/clade rather than sinking them into a large "waste-basket *Oncidium*."

Additionally we here add the comments of Kolanowska & Szlachetko (2016) concerning Chase's transfer of *Odontoglossum* to *Oncidium*. "Detailed analyses of morphology of the species included in phylogenetic analyses conducted by Neubig *et al.* (2012) indicated that the *Odontoglossum* clade consists of some genera easily distinguishable morphologically. We propose to maintain *Cochlioda*, *Solenidiopsis*, *Collare-stuartense* Senghas & Bockemühl, *Symphyglossum* Schltr. and *Odontoglossum* as separate genera, and therefore we postulate to reject Chase *et al.*'s (2008) proposal to include the *Odontoglossum* complex in *Oncidium*."

Relative to this discussion are the comments of Brummitt (2014), "Confusion has arisen in systematics from the failure to appreciate that taxonomy, which groups organisms into ranked taxa (families, genera, etc.), is essentially different from grouping them into clades. Merely because one taxon falls phylogenetically within the clade of another taxon at the same rank does not necessarily mean that it must be included in it taxonomically." Ultimately, neither cladogram nor a phylogenetic tree is a classification and subjective decisions must always be taken to impose the limits and rank of taxa (Brummitt, 1996).

Genera Included In Oncidium by Chase et. al. (2008).



Sigmatostalix Rchb. f.

Solenidiopsis Senghas

Symphyglossum Schltr.



Cochlioda Lindl. Photographs courtesy of Carlos Uribe-Velez.



Oncidium altissimum (Jacq.) Sw. Type of Genus Oncidium Sw.

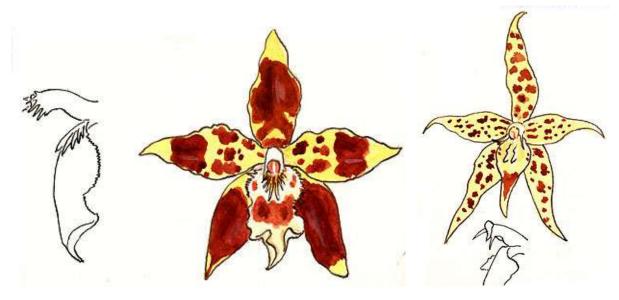
We here agree with Dalström and Kolanowska & Szlachetko to continue to recognize Odontoglossum crispum and reject Oncidium alexandrae (Bateman) Chase & Williams.

Veitch (1887) gives accounts of early collections of *Odontoglossum crispum* from two localities. "Pacho, north of Bogota and Fusagasugá south of Bogota" and states that most of the finest spotted varieties have been received from Pacho and from Fusagasugá have been received the white and mauve tinted forms. Veitch clearly makes a distinction between the plants from the two localities. Veitch also describes plants from among the importations that are of hybrid origin possibly with Odontoglossum odoratum and states that O. odoratum "being remotely concerned in the parentage" implying introgression. However, the reference to O. odoratum is questionable and is probably a misidentification of Odontoglossum gloriosum Linden & Rchb. f.

Crescent (1907) in the Orchid Review in reference to an article by Poirier in the Gardener's Chronicle (1906, ii. Pp 404, 405) is the following: "The author (Poirier) makes some remarks about hybridization, admitting the possibility that some of the spotted forms may be hybrids between *O. crispum* and *O. Adrianae* (natural hybrid between *Odontoglossum nobile* Rchb. f. and *O. luteopurpureum*), and he alludes to *Andersonianum*, *Coradinei* and *Ruckerianum* as species, though they are clearly natural hybrids."



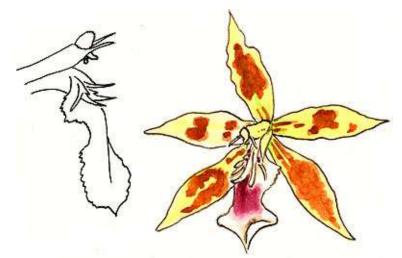
Odontoglossum luteopurpureum Lindl.



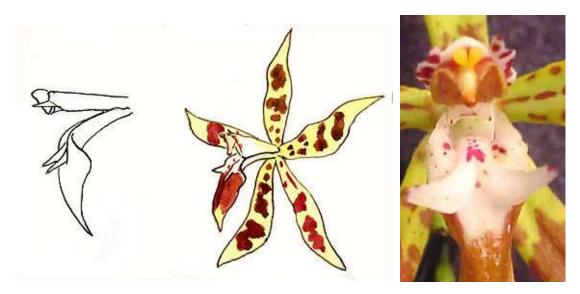
Odontoglossum luteopurpureum Lindl.

Illustrations from archive of Pedro Ortiz Valdivieso.

Odontoglossum gloriosum Linden & Rchb. f.



Odontoglossum wallisii Linden & Rchb. f.



Odontoglossum lindleyanum Rchb. f. & Warsz.

Illustrations and photograph from archive of Pedro Ortiz Valdivieso.

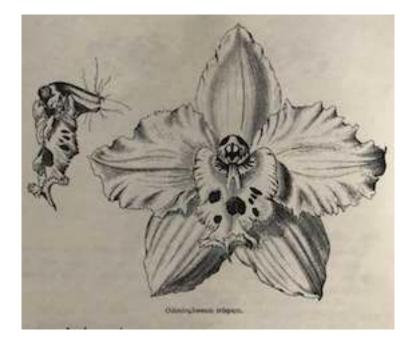


Odontoglossum gloriosum Linden & Rchb. f. Subachoque, department of Cundinamarca.

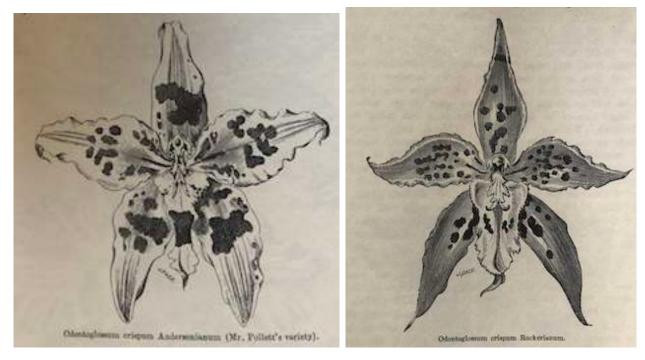
Odontoglossum gloriosum Linden & Rchb. f. department of Boyacá.



Odontoglossum gloriosum Linden & Rchb. f. Variation in crest. Photographs from archive of Pedro Ortiz Valdivieso.



Odontoglossum crispum Lindl. From (Veitch, 1887).



Odontoglossum crispum Andersonianum From (Veitch, 1887).

Odontoglossum crispum Ruckerianum From (Veitch, 1887).

The early literature clearly distinguishes morphologically the localities with the implication that hybrids exist and introgression has occurred. This paper analizes flowers of plants from the localities recognized by Veitch and Poirier; Velez, Fusagasugá (Cabrera), Pacho and an additional locality in the department of Putumayo to determine the range of variation and if any of the populations merit being described as new taxa.

Materals and Method

Four plants representing the range of variation found at each locality were chosen for study: Velez, Santander; Cabrera, Fusagasugá, Cundinamarca; Villa Gomez, Pacho, Cundinamarca; San Francisco, Putumayo. Plants from cultivation were not used because of the extensive line breeding that has been done with selected plants to increase the quality of the flowers.



Icons were constructed of flower from each locality which, included the flower, labellum with column, labellum with crest, close-up of crest and crest side view.

Individual icons were then constructed comparing, from each locality the flowers, labellum with column, labellum with crest, close-up of crest and crest side view.



Odontoglossum crispum Lindl. from Villa Gomez, Pacho.



Odontoglossum crispum Lindl. from Villa Gomez, Pacho.

Discussion

There has been more written on the concept and definition of a species than almost any other subject in botany. The traditional definition of a species is a "diagnosably distinct, reproductively isolated, cohesive, or exclusive groups of organisms" in which "boundaries between species in sympatry are maintained by intrinsic barriers to gene exchange" however, "these boundaries may not be uniform in space, in time, or across the genome" (Harrison and Larson, 2014). According to Baack *et al.* (2007) hybridization, the production of offspring from interspecific matings, occurs in 25% of plant species and 10% to 30% according to Mallet (2005).

Hybridization and introgression in plants has been found to be common. A genome analysis of introgression (the transfer of genes between species mediated primarily by backcrossing) in plants ranging from oaks to orchids has demonstrated that a substantial fraction of their genomes have alleles from related species (Baack *et al.*, 2007).

Hybridization can lead to rapid genomic changes, including chromosomal rearrangements, genome expansion, differential gene expression, and gene silencing (Baack *et al.*, 2007). Hybridization can be a creative evolutionary process, allowing genetic novelties to accumulate faster than through mutation alone (Anderson and Hubricht, 1938; Martinsen *et al.*, 2001). These changes in the genome can lead to rapid selection of new ecological traits that will change the genome structure providing populations a means of coping with environmental change or evolving novel adaptations.

Mutations are rare, around 10^{-8} to 10^{-9} per generation per base pair (Abbott *et al.*, 2013). Therefore, it will take considerable time for novel adaptations to evolve by mutation and natural selection. Hybridization may contribute to speciation through the formation of new hybrid taxa, whereas introgression of a few loci may promote adaptive divergence and facilitate speciation (Mallet, 2005). Hybridization and introgression can lead to speciation in much less time than mutation and natural selection.

Closely related species tend to hybridize more often (Price & Bouvier, 2002; Gourbière & Mallet, 2010) suggesting that hybridization and introgression, via adaptation, are more likely to contribute to speciation in rapidly speciating taxa such as in the genus *Encyclia* Hook. and *Odontoglossum*.

A large amount of introgressed variation is deleterious, and in most cases hybridization has no impact. However, when large numbers of hybridizations occur among closely related species, there is a greater chance that some will result in adaptation and speciation. In the Orchidaceae, the pollination vector is one of the main determining factors if hybridization and introgression results in speciation.

Hybridization and introgression have been found to be common in the subtribe *Laeliinae* and especially in the genus *Encyclia* Hook. (Sauleda & Adams, 1983; 1984; Sauleda, 2016; 2016a). Many natural hybrids occur in the genus *Odontoglossum* and in many species a high degree of variation can be observed possibly due to hybridization and introgression.

A recent addition to the orchid flora of Colombia, *Odontoglossum portillae* Bockemühl (Uribe-Velez & Sauleda, 2020) from Ecuador demonstrates the high degree of variation which occurs in species of the genus *Odontoglossum*.



Variation in *Odontoglossum portillae* Bockemühl from Ecuador. Photograph courtesy of Guido Deburghgraeve.



Odontoglossum crispum Lindl. Plant photographed near type locality in 2010. Locality on holotype: "In the woods between the villages of Zipaquirá and Pacho in the Provincia of Bogotá."

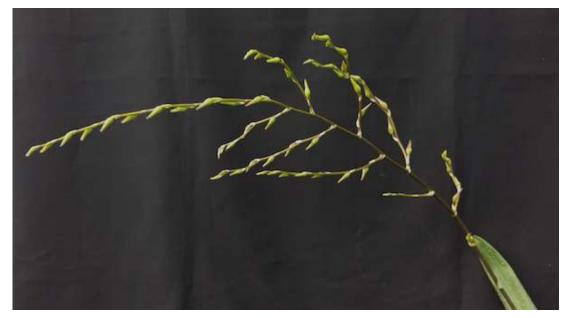
The flowers pictured above closely match the illustration by Veitch of *O. crispum*. However, the type specimen (Holotype, K) is a plant with an inflorescence having several lateral branches, a rare occurrence in the species.



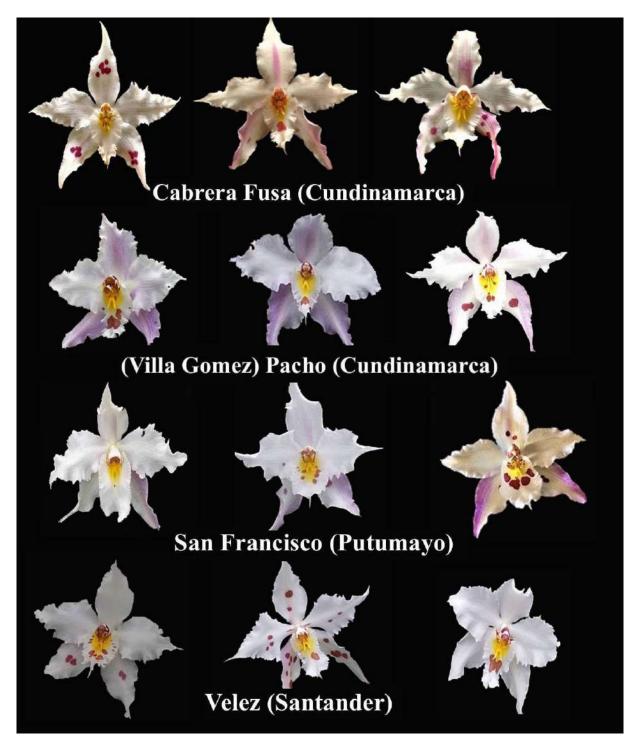
Odontoglossum crispum Lindl. Holotype at K.

The type specimen is atypical of most of the plants found at the localities studied. The majority of the plants do not have branched inflorescences. However, there are plants with branched inflorescences in the Fusagasugá population that match the holotype. These branched inflorescences can be explained as a result of introgression with *O. gloriosum*.



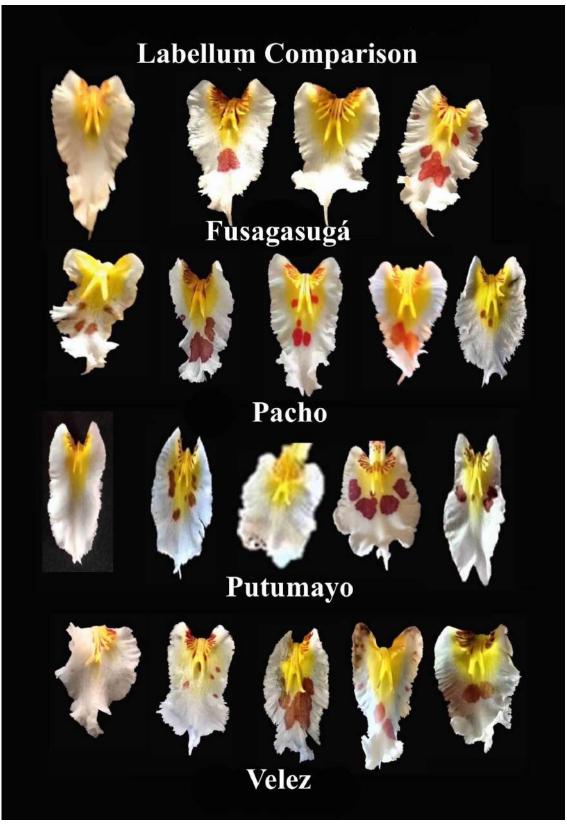


Odontoglossum crispum Lindl. from Fusagasugá. Branched form is nicknamed "cola de pato".



Comparison of Flowers of Representative Individuals from each Locality.

A comparison of representative flowers from each locality tends to support the statement by Poirier that the forms from Fusagasuga' are smaller and have "starry-like flowers". The comment that the finest forms come from Velez is difficult to verify because plants with round petals and full form are found at all the localities except Fusagasuga'. Spotted flowers were found at all the localities. In the general shape the flowers from Fusagasuga' are consistently star-shaped but this difference is not sufficient to merit describing the population as a new taxon. The shape of the labellum, the shape of the sepals and petals varied in each population not demonstrating any clear consistent difference between populations.



Comparison of Shape of the Labellum of the Flowers of Representative Individuals from each Locality.

The size and shape of the labellum was not consistant in each population and therefore, could not be used to characterize the population.

Crest Comparison









Fusagasugá







Pacho









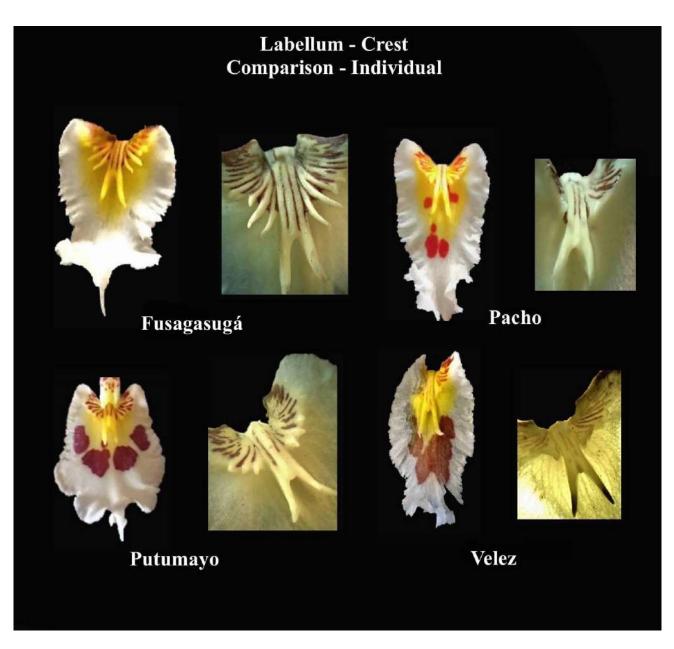


Putumayo



Comparison of the Crest of the Flowers of Representative Individuals from each Locality.

A comparison of representative crests from each population demonstrates a wide range of variation within each population. The lateral lamellae of the callus vary in size and length as do the two central lamellae and a third central lamelle is not always present.



Comparison of Labellum and Crest of Flowers of a Representative Individual from each Locality.





Crest Comparison Side View

Fusagasugá









Pacho



Velez

Comparison of Side View of Crests of Flowers of a Representative Individual from each Locality.



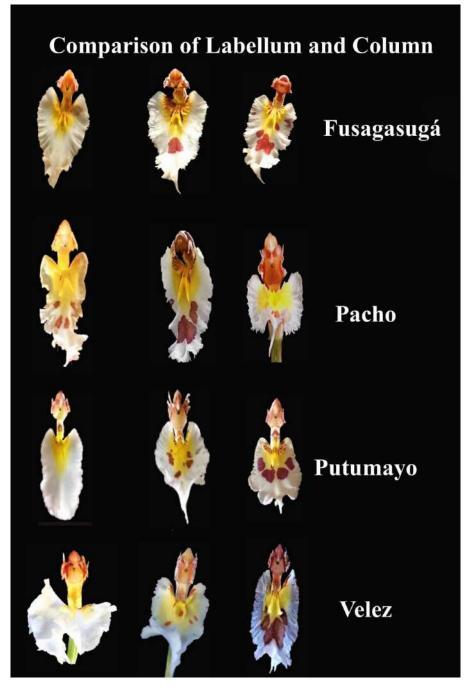
Crest of Odontoglossum nobile Rchb. f. and Odontoglossum gloriosum Linden & Rchb. f.

In populations of *O. crispum* from Pacho in the side view of the crest, introgression involving *O. gloriosum* can be observed. Introgression with *O. nobile* can also be observed in almost all the populations.

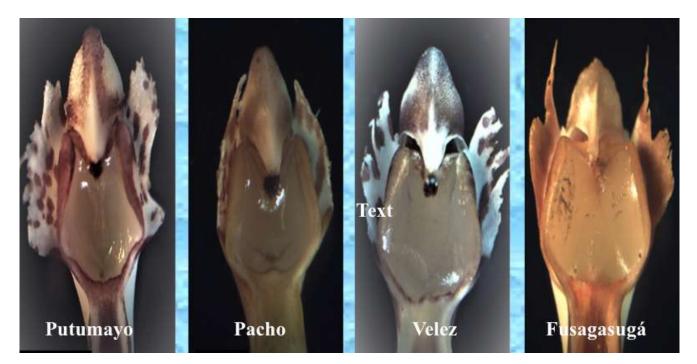


Comparison of Close-up of Crest of Selected Individuals from each Locality.

Many individuals from Pacho and Velez have crests with short lateral fan-like lamellae, where many individuals from Fusagasuga' and Putumayo have longer lateral lamellae and a long central pair of lamellae with a third short central lamella. The crests of some individuals from Pacho lack the pronounced central lamella and the plants from Velez have a short blunt central lamella. The shape of the lamellae of both Fusagasuga' and Putumayo may be due to hybridization and introgression as Poirier suggested. There appear to be definite differences when observing the crests of only selected individuals from the four localities. However, in general the range of variation within each locality is too wide to define each population exactly or describe as new taxa.



Comparison of Labellum and Column of Flowers of Representative Individuals from each Locality.



Comparison of Column Structure of Selected Individuals from each Locality.

Individuals with distinctly different wings on the column can be found in all four populations. The wings of Putumayo and Velez are the most similar with Pacho having the same broad wings but much reduced in size. Some of the wings of the plants from Fusagasuga' have a long thin frontal termination. However, these differences are not consistent in the populations, a wide range exists.

The plants from Fusagasuga' demonstrate the greatest variation in the lamellae of the crest and in the wings of the column. The variation found in the lamellae and starry-like shape may be due to introgression with *O. luteopurpureum* and the frontal projections of the wings due to introgression with *O. gloriosum*.

An analysis of the patterns of the lamellae on the labellum of several species of *Odontoglossum* in the subgenus *Odontoglossum* shows similarities. Similar patterns of the lamellae can be found in individuals of *O. crispum* in the four localities.



Odontoglossum epidendroides Kunth



Odontoglossum cristatellum Rchb. f.



Odontoglossum hallii Lindl.



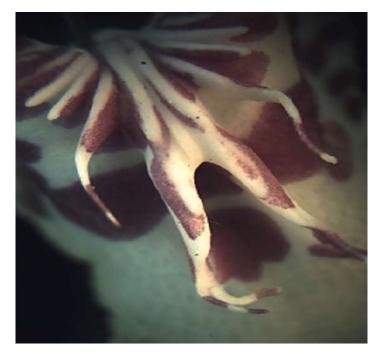
Odontoglossum sceptrum Rchb. f. & Warsz.



Odontoglossum hunnewellianum Rolfe



Odontoglossum paniculatum Dalström & Deburghgr.



Odontoglossum tripudians Rchb. f. & Warsz.

Dalström (2019) makes a reference to a population of *O. crispum* in a project of conservation of orchids called "la palma" near the city of Sibundoy in the department of Putumayo. He reports that *O. crispum* is relatively common along with various other species of *Odontoglossum*. He further reports that in the area photographs were taken of what appear to be several hybrids of *O. crispum*. This would imply that hybridization and possible introgression is occurring also at this locality.

Conclusion

Individuals can be chosen from each locality to demonstrate a distinct pattern of differences. Comparing these selected individuals which, do not represent the total variation of the population, an argument could be made to classify each population as different taxa. These differences in the lamellae and wings of the column can be of great importance when considering the pollinator of each population. The pollinator is the determining factor as to if these populations will evolve into different taxa. A study of the pollinators needs to be made in situ to determine the level of isolation between the populations and if pollinators are selecting distinct forms within the populations.

In conclusion, the four populations can be distinguished if only comparing selected individuals however, if all of the individuals in the population are considered, a wide range of variation occurs without specific consistent characters that could be used to define the populations. Therefore, they are not "diagnosably distinct" enough, to be considered distinct taxa. In addition, the degree of reproductive isolation between the populations is not known. The high degree of variation found at each locality is a direct result of introgression. A report by Florent Claes (1907) in the Orchid Review lists at the Fusagasugá region *O. luteopurpureum*, *O. gloriosum*, *Odontoglossum lindleyanum* Rchb. f. & Warsz. and *Odontoglossum lindenii* Lindl. sympatric with *O. crispum*. In the Pacho region Claes (1907) lists *O. gloriosum*, *O. luteopurpureum*, *O. luteopurpureum*, *O. luteopurpureum*, *O. luteopurpureum*, *O. lutonum* and *Odontoglossum wallisii* Linden & Rchb. f. as sympatric with *O. crispum*. Introgression with these species would account for the variation found in *O. crispum* at the localities.

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