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The Genus *Encyclia* Hook. in the Bahama Archipelago – Species, Hybrids and Introgression Hybrids.

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ABSTRACT

This paper lists and discusses the known species, hybrids and introgression hybrids of *Encyclia* Hook. in the Bahama archipelago.

Historically more has been written on the concept and definition of a species than any other subject in systematic botany. The basic definition 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). Hybridization, the production of viable offspring from interspecific matings, occurs in 25% of plant species according to Baack *et al.* (2007) and 10% to 30% according to Mallet (2005).

Hybridization in plants has been found to be more common than previously realized. Genome-wide analyses of introgression (defined as the transfer of genes between species mediated primarily by backcrossing) in plants ranging from oaks to orchids show that a substantial fraction of their genomes are permeable to 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 is potentially 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 beneficial new phenotypes. Selection can be for new ecological traits that will alter 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). Thus, it is likely to take considerable time for novel adaptations to evolve via mutation and natural selection within a species. Hybridization may contribute to speciation through the formation of new hybrid taxa, whereas introgression of a few loci may promote adaptive divergence and so facilitate speciation (Mallet, 2005). Hybridization and introgression can lead to speciation in much less time.

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*. 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.

Even gene flow between species with large differences in chromosome numbers previously assumed to be reproductively isolated from each other because of strong postzygotic barriers has been found to occur in orchids (Pinheiro, *et al*., 2010).

Hybridization and introgression have been found to be common in the subtribe *Laeliinae* and especially in the genus *Encyclia* Hook. (Sauleda & Adams, 1983; 1984; 1990; Sauleda, 2016; 2016a). The Bahama archipelago is an excellent laboratory to study hybridization, introgression and possible homoploid hybrid speciation in the genus *Encyclia*. There are eleven species distributed throughout the archipelago: *Encyclia androsiana* Sauleda*, Encyclia fehlingii* (Sauleda) Sauleda & Adams*, Encyclia altissima* Schltr.*, Encyclia plicata* (Lindl.) Schltr.*, Encyclia fucata* (Lindl.) Britt. & Millsp.*, Encyclia correllii* Sauleda*, Encyclia rufa* (Lindl.) Britt. & Millsp.*, Encyclia selligera* (Batem. ex Lindl.) Schltr.*, Encyclia caicensis* Sauleda & Adams*, Encyclia inaguensis* Nash ex Britton & Millsp. and *Encyclia withneri* (Sauleda) Sauleda & Adams. Eight of these species are involved in hybridization (73 %) and three demonstrate varying degrees of introgression (27%). Almost three times more hybridization occurs in the encyclias in the archipelago than what Baack *et al.* (2007) and Abbott *et al*. (2013) reported. Eight natural hybrids have been recognized: *Encyclia xgracilis* (Lindl.) Schltr. *(E. correllii x E. fehlingii)* found on Great Abaco and Andros*, Encyclia xknowlesii* Sauleda & Adams *(E. fehlingii x E. plicata)* found on New Providence*, Encyclia xguzinskii Sauleda & Adams (E. altissima x E. plicata)* found on Eleuthera*, Encyclia xhillyerorum* Sauleda & Adams *(E. fehlingii x E. fucata)* found on Andros*, Encyclia xbajamarensis* Sauleda & Adams *(E. correllii x E. rufa)* found on Andros and Great Abaco*, Encyclia xlleidae Sauleda & Adams (E. correllii x E. plicata))* found on New Providence*, Encyclia xraganii* Sauleda & Adams *(E. altissima x E. correllii)* found on Andros*,* an unnamed hybrid of *E. altissima* x *Encyclia inaguensis* and an introgression hybrid *Encyclia xadamsii* Sauleda (*E. androsiana x E. fehlingii*) found on Andros and Great Abaco *(*Sauleda, 2016). Introgression resulting in phenotypic variation is apparent in *E. correllii, E. xadamsii* and *E. plicata.* The other hybrids are isolated occurances and introgression does not appear to be occurring at this time.

Populations of *E. plicata* demonstrate a high level of phenotypic variation throughout the archipelago. However, on Andros Island along the edge of Fresh Creek a population occured that exhibited extreme variation. Although *E. phoenicea* has not been reported for the Bahama archipelago its influence is clearly present in the color and shape of the labellum in the Fresh Creek population. The usually reflexed or pleated midlobe of the labellum and the two fleshy pads spreading from the base of the disc, dominant characters of *E. plicata,* are usually found in the hybrids of *E. plicata*. *Encyclia plicata* is very dominant as evidenced by the natural hybrids that have been reported. Additionally, the artificial hybrid between *E. plicata* and *E. phoenicea* also clearly demonstrate this dominance. *Encyclia plicata* in Cuba exhibits a high level of phenotypic variation also due to hybridization and introgression.

One of the most common and widespread species of *Encyclia* in the Bahama archipelago was named *Epidendrum gracile* Lindl. and later transferred by Schlechter to *Encyclia* (*Encyclia gracilis* (Lindl.) Schltr.). Sauleda (2012) determined that this common species did not match the plate or the type specimen of *E. gracile*. The plate and type represent a natural hybrid of the common species crossed with *E. fehlingii,* previously named *Encyclia xlucayana* Sauleda and Adams. Therefore, the common species did not have a name; *Encyclia correllii* was published by Sauleda (2012) as the name for the population.

Encyclia gracilis (*E. gracile*) was first reported for Cuba by Acuña (1938) from Baracoa. Leon (1946) also reported *E. gracile* from Baracoa, but no corroborating specimen was cited by either author. Leon

may have been repeating Acuña's citation. The only specimen labeled *Epidendrum gracile* from Cuba that Acuña and Leon may have seen, was collected by J. G. Jack in 1928, at Santa Clara, Cuba (NY). However, the Jack specimen is not *E. gracile*. It was annotated as *Encyclia* without a species determination by J. D. Ackerman and annotated as *Encyclia bipapularis* (Rchb. f.) Acuña by R. L. Dressler.

Dietrich (1984) reported *Encyclia gracilis* for Cuba based on a misdetermination (Ackerman, 2014). Dietrich listed *Encyclia gracilis* auct non. (Lindl.) Schltr. as a synonym for *Encyclia moebusii* H. Dietr. Obviously, Dietrich confused *E. moebusii* with *E. gracilis*, a very different species. The reports by Acuña, Leon and Dietrich of *E. correllii* or *E. xgracilis* in Cuba cannot be corroborated.

Specimens were found at AMES and NY collected by Howard *et al*. in 1951, labeled *Epidendrum gracile*, from Santa Clara, Cuba. However, the specimen is not *E. gracile* and has been annotated by both R. L. Dressler and J. D. Ackerman as *Encyclia phoenicea* (Lindl.) Neumann. Another specimen at P labeled *E. gracile* (TYPE) from Mexico appears to be *Encyclia bractescens* (Lindl.) Hoehne.

Greuter *et al.* (2016) listed *E. gracilis* as occurring in three localities in Cuba (Provincia Ciego de Avila, Provincia Camaguey, and Provincia Las Tunas). What Greuter *et al.* (2016) are referring to, as *E. gracilis* is not clear. Sauleda (2012) made the determination that *E. gracilis* was a natural hybrid and published *E. correllii* as the proper name for the common species. The use of the epithet *E. gracilis* by Greuter *et al*. (2016) shows either a lack of knowledge of the literature or understanding of either taxa. However, in their treatment of the flora of Cuba, Greuter *et al.* (2016) under *Encyclia phoenicea* (Lindl.) Neumann list as synonyms species validly published after 2012, which are not synonyms of *E. phoenicea* (*Encyclia hamiltonii* Sauleda and Esperón and *Encyclia havanensis* O. Bello, *et al*.). The epithet *E. gracilis* is not the proper epithet to use in light of the latest literature.

Encyclia correllii has a distinctive character that is rare in the orchid family. The bases of the leaves lack an abscission layer. Consequently the leaves never abscise. All of the natural hybrids and introgression hybrids of *E. correllii* also lack the abscission layer making them easy to identify using live material or herbarium specimens. The greatest amount of hybridization (four natural hybrids) and introgression in the Bahama archipelago occurs with this species. However, although the hybrids are easy to identify, the other species involved in introgression in the hybrids are not easily identified. In the Bahama archipelago this species shows the greatest amount of phenotypic variation but no phenotype is clearly dominant.

Recently the junior author observed on Cayo Ballenato, Bahia de Neuvitas, Camaguey, Cuba plants with leaves that did not abscise growing sympatrically with *E. altissima*. The plants were not in flower and a proper identification could not be made.

After an extensive search of the major herbaria in the US and Europe no herbarium specimens matching *E. xgracilis* or *E. correllii* have been found from Cuba. As far as can be determined at this time, there is no evidence that *E. correllii* or *E. xgracilis* are found in Cuba although the possibility definitely exists.

In the literature, *Encyclia tampensis* has had a long history in the Bahama archipelago. It has been reported for the Bahama archipelago and Cuba by numerous authors (Ames, 1924; Acuña, 1938; Leon, 1946; Correll, 1950; Sauleda and Adams, 1982; 1983; Dietrich, 1985; Diaz, 1988; Greuter *et al.,* 2016). However, the reports for Cuba could be any one of several species similar to *E. tampensis*.

Originally *E. tampensis* was believed to be a variable species (Sauleda and Adams, 1979; 1982; 1983; Withner, 1996)). At first, Sauleda (1977) determined that the population in the Bahama

archipelago included another species, *E. fehlingii* (Sauleda) Sauleda and Adams. Recently, Sauleda (2012) determined that yet another species, *E. androsiana* was also being included in the concept of *E. tampensis* in the Bahama archipelago. Results of self-pollination of both *E. fehlingii* and *E. androsiana* proved that they are both pure species with little or no introgression (Sauleda, 2016). What was being called *E. tampensis* in the Bahama archipelago was actually a natural hybrid, *E. xadamsii*, of *E. fehlingii* and *E. androsiana* with introgression on both islands (Sauleda, 2016).

Self-pollination studies indicate that *E. tampensis* in Florida, where the type was collected, is a complex hybrid swarm involving *E. androsiana, E. fehlingii* and other undetermined species (Sauleda, 2016). Withner (1969) noted that the Florida plants of *E. tampensis* were phenotypically different from the Bahamian plants. Withner (1996) also noted that most of the plants referred to *E. tampensis* in Cuba were *Encyclia oxypetala* (Lindley) Acuña or *E. fucata* (Lindl.) Schltr. Ackerman (2014) states: "On a field trip to Holguín Province of Cuba in 1997, we encountered plants, in full flower, that had been traditionally called *E. tampensis*, but Bob Dressler immediately proclaimed them quite different from the Florida plants." The population of *E. tampensis* in Cuba is a misidentification and the Florida population is genetically different from the population in the Bahama archipelago.

The introgression hybrid of *E. androsiana* and *E. fehlingii* backcrosses to *E. androsiana* on Andros Island, but backcrosses to *E. fehlingii* on Great Abaco. *Encyclia androsiana* is presently rare or possibly extinct in the Bahama archipelago having been found originally only on Driggs Hill, South Andros Island. The plants grew epiphytically on large trees, which have been removed. *Encyclia fehlingii* was sympatric with *E. androsiana* on Driggs Hill, but on subsequent trips to Driggs Hill plants of *E. androsiana* were not located. However, plants of *E. xadamsii* are still common in the area around Driggs Hill. Possibly homoploid hybrid speciation is starting to occur with the introgression hybrids on the respective islands.

At the present time a comprehensive treatment of the species of *Encyclia* in Cuba is underway but has not been completed. However, based on the present information, the Bahama archipelago only shares four species of the eleven species of *Encyclia* with Cuba. It can be theorized that most of the species in the Bahama archipelago migrated from Cuba starting around 30,000 y.b.p. when the sea levels started to drop. At that time the sea levels were 7-8 m above present levels (Richards, 1975). The elevations of the islands on the Bahama Bank varied from 10 m above sea level on North Andros to 54 m above sea level on Cat Island and to 40 m above sea level on Providenciales on the Caicos Bank. At 15,000 y.b.p. the sea levels reached a level approximately 150 feet lower than present (Bloom, 1971; Emery, *et al*.). Although a land bridge never occurred, the distance between the Bahama Bank and Cuba was only 40 km. Three species, *E. fucata, E. plicata* and *E. altissima* of the four reported also for Cuba and are common in Cuba. *Encyclia rufa* has also been found in Cuba but appears to be rare. The only specimen extant of *E. rufa* from Cuba is at AMES collected at Nuevitas, Camaguey Prov., by Camacho in 1952. Since the Camacho collection, *E. rufa* has only been observed one other time in Cuba growing on the ground in a dry deciduous forest in the Peninsula Nuevas Grandes, Camaguey (Esperon and Sauleda, 2012). In addition, J. K. Small collected *E. rufa* in Florida in a hammock north of Eau Galle, Brevard County, Florida and the specimen is extant in NY (*Small et al., 12938*, 24 May 1926). Other than this single plant no viable population has been found in Florida.

Based on the information known, the species *E. fehlingii, E. androsiana, E. correllii, E. inaguensis* and *E. caicensis* presently appear to be endemic to the Bahama archipelago. *Encyclia caicensis* is found only on the Turks and Caicos Islands. Two other species are unusual occurances in the Bahama archipelago, *E. selligera* and *E. withneri. Encyclia selligera* a species usually found on the Pacific side of Central America was found on South Andros, as was *E. withneri*. *Encyclia withneri* does not appear to be related to any of the Caribbean species. It is very similar to several Central American species. The connection of Central America to the Bahama archipelago is not easy to explain.

It can be theorized that from 30,000 y.b.p. to present six species evolved in the Bahama Islands. However, it can also be theorized that all the species evolved in Cuba, migrated to the Bahama Islands and extinction occurred in Cuba. The fact that *E. rufa* is the second most common species in the Bahama archipelago but rare in Cuba could indicate that extinction is occurring in Cuba. Most orchids are sensitive to temperature changes; just a few degrees of change can restrict the growth and flowering of a species. In addition temperature changes can also exclude a pollinator leading to extinction. *Encyclia fehlingii* and *E. androsiana* are closely related to several species in Cuba and vegetatively are very similar possibly indicating they evolved more recently from a common ancestor. Also *E. altissima, E. inaguensis* and *E. caicensis* are very similar vegetatively also indicating a possible common ancestor. It could also be theorized that these similar species evolved through hybridization and introgression.

Encyclia xraganii consists of a large stable population along the airport runway at Congo Town, South Andros (Sauleda and Adams, 1981). The plants exhibit the lack of abscission layer typical of *E. correllii* and the long thin leaves and pseudobulbs typical of *E. altissima*. The individuals in the population appear to be very similar and intermediate between the parents without signs of introgression. All of the other natural hybrids appear to be isolated plants without obvious signs of introgression.

There does not appear to be any correlation between the distribution on the islands of a species and the number of natural hybrids or degree of introgression that occurs with that species. *Encyclia altissima* has the widest distribution, occurring on twenty-one islands, followed by *E. rufa* occurring on twenty islands. *Encyclia altissima* has contributed to three natural hybrids and *E. rufa* only one natural hybrid. *Encyclia fehlingii* occurs on seven islands and has contributed to four natural hybrids. None of these species demonstrates any clear signs of introgression. However, *E. correllii*, which occurs on only twelve islands, has contributed to four natural hybrids and introgression has obviously occurred. *Encyclia plicata*, which has the narrowest distribution, only occurring on three islands, has contributed to three natural hybrids and demonstrates signs of introgression.

Endemism has been extensively studied in the Bahama archipelago. In the most recent studies Acevedo *et al.* (2012) determined that were are 101 endemic species (9.4%) of seed plants in the Bahama archipelago. Fried *et al*. (2014) determined that after all the recent taxonomic changes that only 89 species (6%) are endemic. The three genera with the highest number of endemics are *Agave* with eight species, *Euphorbia* with seven species and *Encyclia* and *Spermacoce* each have six species (Fried *et al*., 2014). However, in the light of the most recent research there are eleven species of *Encyclia* in the Bahama archipelago and seven are endemic. That computes to 64%, a number much higher than the average.

The results of this study of the encyclias of the Bahama archipelago confirms that, hybridization and introgression are actively occurring processes and possibly a more widespread evolutionary phenomenon than previously believed.

List of Species

Encyclia altissima Schltr.
Encyclia androsiana Sauleda
Encyclia caicensis Sauleda & Adams
Encyclia correllii Sauleda
Encyclia fehlingii (Sauleda) Sauleda & Adams
Encyclia fucata (Lindl.) Britt. & Millsp.
Encyclia inaguensis Nash ex Britton & Millsp.
Encyclia plicata (Lindl.) Schltr.
Encyclia rufa (Lindl.) Britt. & Millsp.
Encyclia selligera (Batem. ex Lindl.) Schltr.
Encyclia withneri (Sauleda) Sauleda & Adams

Natural Hybrids

Encyclia xadamsii Sauleda (*E. androsiana x E. fehlingii*) - Andros and Great Abaco
Encyclia xbajamarensis Sauleda & Adams *(E. correllii x E. rufa)* - Andros and Great Abaco
Encyclia xgracilis (Lindl.) Schltr. *(E. correllii x E. fehlingii)* - Great Abaco and Andros
Encyclia xguzinskii Sauleda & Adams (E. altissima x E. plicata) – Eleuthera
Encyclia xhillyerorum Sauleda & Adams *(E. fehlingii x E. fucata)* – Andros
Encyclia xknowlesii Sauleda & Adams *(E. fehlingii x E. plicata)* - New Providence
Encyclia xlleidae Sauleda & Adams (E. correllii x E. plicata) - New Providence
Encyclia xraganii Sauleda & Adams *(E. altissima x E. correllii)* – Andros
E. altissima x *Encyclia inaguensis* - an unnamed hybrid

Islands, Island Area and Number of Species/Island

ISLAND	Area km. sq.	Number of species	*E. altissima*	*E. rufa*	*E. correllii*	*E. fehlingii*	*E. caicensis*	*E. fucata*	*E. inaguensis*	*E. plicata*	*E. selligera*	*E. androsiana*	*E. withneri*
Andros (North and South)	5,184	9	■	■	■	■		■		■	■	■	■
Great Inagua	1,544	3	■	■	■								
Great and Little Abaco	1,146	6	■	■	■	■		■		■			
Grand Bahama	1,096	5	■	■	■	■		■					
Long Island	596	3	■	■	■								
Eleuthera	518	3	■	■	■								
Acklin's Island	497	1	■										
Cat Island	389	3	■	■	■								
Mayaguana	285	1	■										
Great Exuma	250	4	■	■	■				■				
Crooked Island	241	3	■	■	■								
New Providence	207	5	■	■	■	■				■			
San Salvador	163	2	■	■									
Little Inagua	127	3	■	■					■				
Rum Cay	78	1	■										
Little Exuma	29	3	■	■	■								
Norman's Cay, Exuma Chain	3	2	■		■								
Staniel Cay, Exuma Chain	1.4	1	■										
North Bimini	9	2		■		■							
South Bimini	6	3		■		■		■					
Great Harbor Cay, Berry Islands	23	1		■									
Frazer's Hog Cay, Berry Islands	7.5	2		■		■							
Grand Caicos	144	4	■	■	■				■				
North Caicos	41	4	■	■			■		■				
South Caicos	8.2	1					■						
Providenciales	98	3	■	■					■				

Hybrids by Island

ISLAND	*E. x bajamarensis*	*E. x gracilis*	*E. x knowlesii*	*E. x guzinskii*	*E. x adamsii*	*E. x hillyerorum*	*E. x lleidae*	*E. x raganii*
Andros	■	■			■	■		■
Great and Little Abaco	■	■			■			
Eleuthera				■				
Cat Island	■							
New Providence			■				■	

Encyclia caicensis
Type plant

Encyclia inaguensis

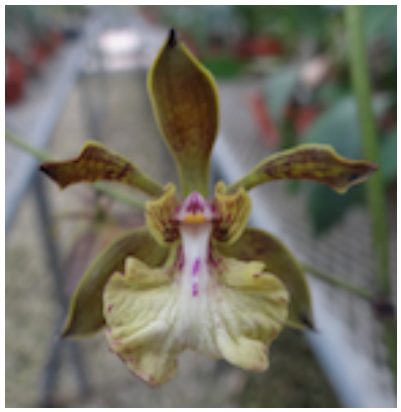
Encyclia fehlingii
Type plant

Encyclia androsiana
Type plant

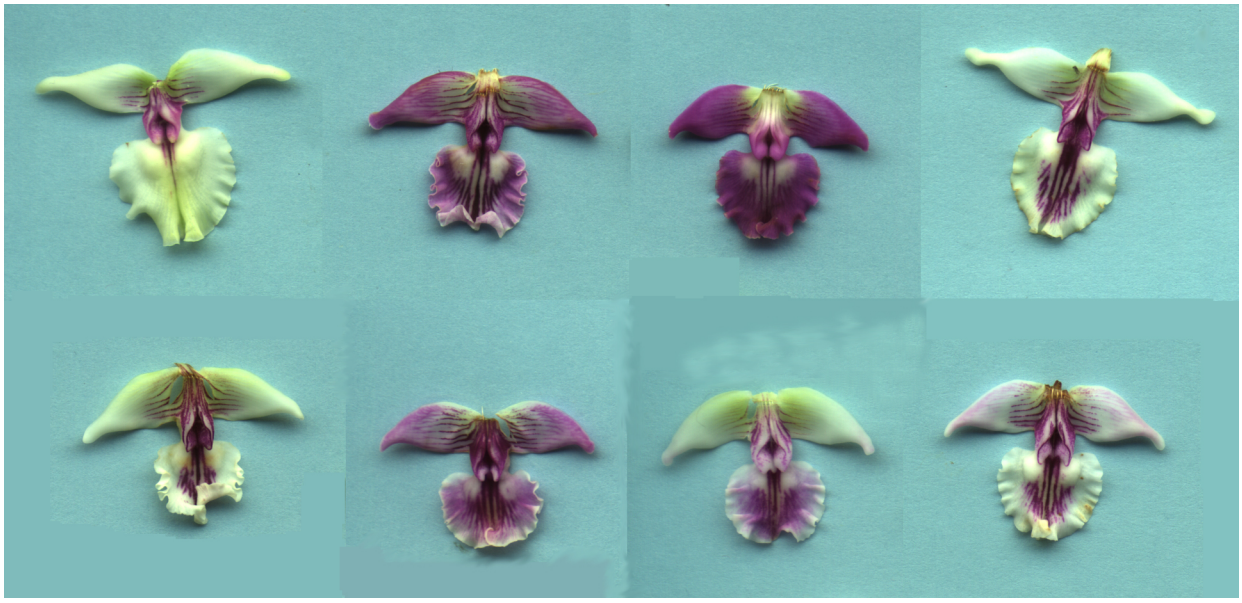
Encyclia fucata

Encyclia withneri
Type plant

Distinct color forms of *Encyclia rufa.*



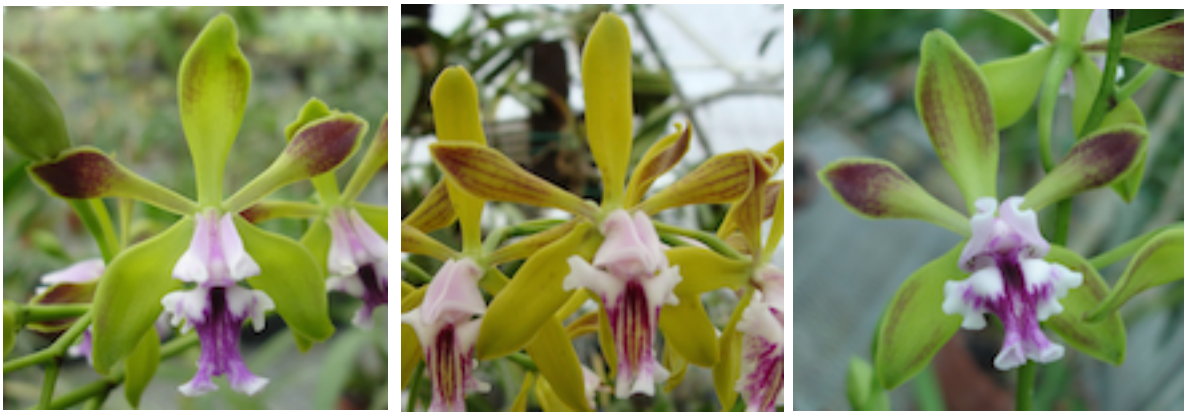
Variation in *Encyclia altissima.*



Variation in labella of *Encyclia plicata* from Fresh Creek, Andros Island, population.

Labellum of *Encyclia phoenicea* from Cayman Islands.

Encyclia plicata from Cuba.



Variation in *Encyclia plicata* from the Bahama archipelago.

Encyclia plicata possible introgression hybrid.

Artificial hybrids of *E. plicata* and *E. phoenicea* demonstrating dominance of *E. plicata*.

Encyclia xknowlesii – Type plant
(E. fehlingii x *E. plicata)*.

Encyclia xlleidae Natural Hybrid
(E. correllii x *E. plicata)* – Type plant.

Encyclia xlleidae Artificial Hybrid
(E. correllii x *E. plicata).*

Encyclia xguzinskii – Type plant
(E. altissima x *E. plicata).*

Natural hybrid of *E. altissima*
x *Encyclia inaguensis.*

Encyclia xgracilis, previously named *Encyclia xlucayana*
(E. correllii x *E. fehlingii*).

Epidendrum gracile Lindl., flower from Lindley plate.

Encyclia xraganii plant lacking abscission layer at base of leaves.

Encyclia xraganii
(E. altissima x *E. correllii).*

Encyclia xraganii – Type plant
(E. altissima x *E. correllii).*

Encyclia xbajamarensis
(E. correllii x *E. rufa).*

Encyclia xbajamarensis – Type plant
(E. correllii x *E. rufa).*

Variation in *Encyclia correllii.*

Encyclia correllii with introgression. All plants lacking an abscission layer.




Encyclia xadamsii introgression hybrid of *E. androsiana* and *E. fehlingii* from Andros Island previously reported as *Encyclia tampensis.*



Encyclia xadamsii introgression hybrid of *E. androsiana* and *E. fehlingii* from Great Abaco, previously reported as *Encyclia tampensis.*

Encyclia altissima in situ.

Encyclia caicensis in situ.

Encyclia inaguensis in situ.

Artificial intergeneric hybrid (*E. plicata* X Catyclia El Hatillo) demonstrating dominance of *E. plicata*. Catyclia El Hatillo is *E. tampensis* crossed with Cattleya *mossiae*.

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Note: In 1742, seven years after writing "*nullae dantur species novae* " (there are no new species) (Linnaeus, C., Systema naturae. 1735.) Carolus Linnaeus was brought a fertile floral mutant of *Linaria* that he called "*Peloria*". The unusual floral structure convinced Linnaeus that the plant was of hybrid origin, and the fertility of *Peloria* and other hybrids led Linnaeus to abandon his earlier certainty in the fixed nature of species. Instead, he proposed the radical evolutionary hypothesis that new species could arise via hybridization (Larson, J. L., The species concept of Linnaeus. 1968.)