

February 2, 2025

Hybridization and Introgression in the Genus *Encyclia* Hook. (Orchidaceae).

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Abstract

A comparison of the processes of speciation by hybridization and introgression in the genus *Encyclia* Hook. (Orchidaceae) in populations in Colombia, Bahama Islands and Florida.

Introduction

Changes in the genome due to hybridization and introgression can lead to rapid selection of new phenotypes. Mutations are rare, around 10^{-8} to 10^{-9} per generation per base pair (Abbott *et al.*, 2013) resulting in taking considerable time for new phenotypes to evolve via mutation and natural selection within a population.

Hybridization contributes to speciation by the formation of new hybrid taxa, whereas introgression of a few loci may promote adaptive divergence and so facilitate speciation (Mallet, 2005). A large amount of introgressed variation can be deleterious or non productive, and in most cases hybridization has no impact. However, when a large number of hybridizations and introgression occurs among closely related species, such as occurs in the Bahama Islands and Florida in the genus *Encyclia* Hook. there is a greater chance that some will result in adaptation and eventually speciation.

Hybridization is common in the genus *Encyclia* Hook. (Sauleda & Adams, 1983; 1984; 1990; Sauleda, 2016) and several distinct outcomes (Abbott, 2013) are possible. Only a single isolated individual resulting from hybridization can be found without further reproduction occurring (Sauleda & Adams, 1990). In Colombia single occurring hybrids can be found without any evidence of introgression such as *Encyclia xpadreortizii* Sauleda (*Encyclia ceratistes* (Lindl.) Schltr. X *Encyclia diurna* (Jacq.) Schltr.) and *Encyclia xcordistes* Sauleda (*Encyclia cordigera* (Kunth) Dressler X *Encyclia ceratistes* (Lindl.) Schltr.). In many cases a hybrid results with introgression in only one direction. This is what appears to have occurred with *Encyclia replicata* (Lindl. & Paxt.) Schltr in Colombia (Sauleda, 2016b). *Encyclia replicata* hybridized with *Encyclia ceratistes* (Lindl.) Schltr. and introgression has occurred back to *E. replicata*. This accounts for the variation in lip shape and color observed in individuals of the population. The publication of the three names for the same population was due to the minimal amount of live material available to properly evaluate the range of natural variation.

In the Bahama archipelago there are eleven species of *Encyclia* 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. Nine of these eleven species are involved in hybridization (82 %) and three demonstrate varying degrees of introgression (27%). Almost three times more hybridization occurs in the encyclias in the archipelago than what Abbott *et al.* (2013) report for other plants.

Encyclia fucata has a limited range in the Bahama archipelago and does not appear to have any introgression. Two other species in the Bahama archipelago appear to have connections with Central America. *Encyclia selligera* is a species found in Central America and *Encyclia withneri* is similar to several Central American species. Very few plants of both species were observed. *Encyclia selligera* did not demonstrate any variation and *E. withneri* demonstrated limited variation with no evidence of introgression.

Nine 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 and *Encyclia xadamsii* Sauleda (*E. androsiana* x *E. fehlingii*) found on Andros and Great Abaco (Sauleda, 2016). *Encyclia xesperonii* Rodr. Seijo and Sauleda (*E. altissima* x *E. rufa*) occurs in the Bahama Islands as a natural hybrid without apparent introgression on Andros, Great Abaco, Cat Island (Rodr. Seijo & Sauleda, 2017). This hybrid is also found in Camaguey, Cuba. At this locality introgression is occurring between the hybrid and other sympatric species (Rodr. Seijo & Sauleda, 2017). Introgression resulting in phenotypic variation is apparent in *E. correllii*, *E. xadamsii* and *E. plicata*. The other hybrids are isolated occurrences and introgression does not appear to be occurring at this time.

In the Turks and Caicos islands an undescribed natural hybrid, appears to be present between *E. caicensis* and *E. rufa* with introgression back to *E. caicensis*. The flowers strongly resemble *E. caicensis* but the yellow color of the flowers, the arrangement of the flowers on the inflorescence and broad leaves are suggestive of *E. rufa*. Also a natural hybrid between *E. altissima* and *E. inaguensis* undescribed has been found.

Introgression resulting in phenotypic variation is apparent in *E. correllii*, *E. xadamsii* and *E. plicata*. The other hybrids in the Bahama Islands with the exception of *E. xraganii* are isolated occurrences and introgression is not apparent. *Encyclia xraganii* on Andros Island, Bahama Islands is a large stable population that is reproducing and operating as a species. This is a prime example of potential speciation through hybridization.

Encyclia tampensis (Lindl.) Small in Florida appears to be an example of a hybrid swarm composed of more than two species (Sauleda, 2016c).

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 (Sauleda & Esperon, 2016d). In the Bahama Islands *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* to two natural hybrid. *Encyclia fehlingii* occurs on seven islands and has contributed to four natural hybrids. None of these species demonstrate any clear signs of introgression. However, *E. correllii*, which occurs on 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.

Encyclia correllii has produced four natural hybrids and is the species with the greatest phenotypic variation due to introgression. It has by far the widest range of variation of the species of *Encyclia* in the Bahama Islands. It is comparable to *E. tampensis* in Florida in degree of variation.

However *tampensis* is a hybrid swarm resulting from hybridization of three or more species. The variation in these species is due to hybridization and many of the morphs resemble what appears to be the original species. In contrast, the high degree of variation in *E. correllii* is a result of introgression with sympatric species. In the case of *E. tampensis* the parental species are no longer present in Florida. However, in Seven Palm Lake in the Everglades National Park, Florida, morphs can be observed that resemble species of *Encyclia* that are found in Cuba.

All of the processes of hybridization and introgression that lead to speciation can be observed in the genus *Encyclia* on the Bahama Islands and Florida. This confirms that hybridization and introgression are actively occurring processes and possibly a more widespread evolutionary phenomenon than previously believed.



Encyclia ceratistes



Morph of *Encyclia replicata* demonstrating introgression with *Encyclia ceratistes*.



Variation in *Encyclia correllii* Saulea of morphs with less introgression.



Variation in *Encyclia correllii* Saulea of morphs with less introgression.



Variation in *Encyclia correllii* demonstrating introgression.



Encyclia fehlingii



Encyclia rufa



Encyclia altissima

Three species involved in the hybridization with *Encyclia correllii*.



Morph of *Encyclia correllii* demonstrating possible hybridization with *Encyclia phoenicea* (Lindl.) Neumann. indicating that *E. phoenicea* may have occurred in the Bahama Islands.



Encyclia phoenicea (Lindl.) Neumann. Plant from Grand Cayman Island.

Natural hybrids



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



Encyclia xgracilis (*E. correllii* x *E. fehlingii*).



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



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



Encyclia xknowlesii
(*E. fehlingii* x *E. plicata*).



Encyclia xguzinskii
(*E. altissima* x *E. plicata*).



Undescribed natural hybrid
(*E. altissima* x *E. inaguensis*).



Encyclia caicensis.



Possible natural hybrid of *Encyclia caicensis* x *Encyclia rufa*, undescribed with introgression.



Encyclia plicata from Bahama Islands.



Encyclia plicata from Cuba.

Difference between *E. plicata* from the Bahama Islands and Cuba due to introgression with different species.



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



Variation in *Encyclia androsiana*. No introgression.



Encyclia xadamsii (*E. androsiana* x *E. fehlingii*) from Andros Island, Bahama Islands, with introgression.



Encyclia withnerii from Drigg's Hill, Andros Island, Bahamas.



Encyclia selligera from Drigg's Hill, Andros Island, Bahamas.



Variation resulting in progeny from self pollination of *Encyclia tampensis* from Florida.



Photographs of variation in *Encyclia tampensis* taken in situ at Seven Palm Lake, Miami-Dade County, Florida.

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