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Author: Arango, Octavio

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Principles governing F1 hybridization in the genera *Aeonium* and *Greenovia* in La Gomera, Canary Islands

Octavio Arango¹

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Abstract: A phytochorological and ecobiological study of the nine species, two subspecies and two varieties of the genera *Aeonium* and *Greenovia* in La Gomera is carried out, with special attention to F1 hybridization in nature. To the ten hybrids already described on the island, seven new hybrids were discovered, which are the subject of a separate publication. In all the known hybrids I determined whether the parents were sympatric or allopatric. The geographical coincidence of the parents was a sine qua non requirement for hybridization to occur in all the hybrids known so far, since pollen transfer by biotic and abiotic agents does not function between disjunct areas. The two prezygotic reproductive barriers that currently prevent interspecific hybridization in *Aeonium* or intergeneric hybridization between *Aeonium* and *Greenovia* are the geographic separation of populations and the different flowering times. The ability to survive and reproduce successfully of F1 hybrids in *Aeonium* and *Greenovia* is usually lower than that of the parent species and they generally disappear from the environment in the first filial generation without leaving offspring. The fundamental principles that govern F1 hybridization in La Gomera are extracted, and after verifying that they were also fulfilled in the other mountainous islands, they were synthesized in eight principles, which provide an updated vision of hybridization in the genus *Aeonium*.

Keywords: *Aeonium*, Canary Islands, chorology, ecology, *Greenovia*, hybridization, La Gomera, reproductive biology, sympatry

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Introduction

This research is based on the phytochorological study of Voggenreiter (1999), where he describes in detail the distribution of all species, subspecies, and hybrids that compose the genera *Aeonium* Webb & Berthel. and *Greenovia* Webb & Berthel. in La Gomera, and locates cartographically each of the taxa in grids of 1 × 1 km. In addition, he establishes the relationships of the species with the hybrids known up to that moment. His study shows how the taxa of both genera are distributed throughout practically the entire island, and more than half of them are endemic to La Gomera. The remarkable adaptability of these plants has allowed them to colonize the large variety of ecological niches on the island, making it an optimal natural laboratory for chorological, ecological, and reproductive biology studies.

The genus *Greenovia* was recognized as different from *Aeonium* a long time ago (1836–1840) based on significant morphological characters, such as flower parts or placentation. With the introduction of molecular studies two facts appeared. First, the *Greenovia* members formed a tight monophyletic cluster and, second, this cluster ap-

peared within the larger *Aeonium* group (Mes 1995; Jorgensen & Frydenberg 1999; Mort & al. 2002). Since it is desirable that a genus should be monophyletic, Mes suggested to include *Greenovia* as a section of *Aeonium* and therefore *Aeonium* was not paraphyletic anymore.

Both facts have been maintained as more detailed and robust trees were built, the latest and most complete being that of Messerschmid & al. (2023). Changing the name of *Greenovia* to *Aeonium* is certainly an easy way out. However, I think it is premature. Despite the many nucleotides included in the latter study, the tree was not well resolved. And several taxa appear in different branches when the trees are built with different criteria. This means that there still is not enough information to properly describe the group phylogeny. Until the branching order of the whole group is well established, changing the name of a genus is premature. And several authors have gone along this line (Lodé 2010; Schönfelder & Schönfelder 2018; Sauerbier & al. 2023).

Of all the genera that make up the rich and varied flora of the Canary Islands, *Aeonium* has the largest number of species and subspecies (Bramwell & Bramwell 2001; Acebes-Ginovés & al. 2009; Schönfelder & Schönfelder

¹ Cl. Loreto 24–26, Escalera B, 4° 2', 08029 Barcelona, Spain.

Author for correspondence: Octavio Arango, oja.oja@hotmail.com

2018; BIOTA 2023; Sauerbier & al. 2023) and it has generated the largest number of natural hybrids in the entire archipelago. In addition, intergeneric hybrids are formed frequently between *Aeonium* and *Greenovia*. The works of Praeger (1929, 1932) were the seminal papers on hybridization in the genus *Aeonium* in the Canary Islands. They were later joined by the publications of Lems (1960), Liu (1989), Marrero (1992), Voggenreiter (1999), and Jorgensen & Olsen (2001). Since then, very little progress has been made in understanding the eco-biological mechanisms governing hybridization in the genera *Aeonium* and *Greenovia*, with most subsequent publications focusing only on the taxonomic aspects of hybrids.

Marrero (1992) established three different groups of plants in the Canary flora according to the hybridization process, depending on the level of differentiation that the taxa had reached during the geographic isolation to which they had been subjected, and the capacity to hybridize when they coincide again. In addition, he analysed the effectiveness of the reproductive barriers acquired during isolation and the viability of the hybrids they generate. The first group includes allopatric species that normally hybridize when they meet again due to various factors, such as *Cheirolophus* Cass., *Crambe* L. and *Limonium* Mill. The second group includes isolated or sympatric species, in which hybridization is more or less viable depending on the taxa, such as *Echium* L., *Micromeria* Benth. and *Sideritis* L. And the third group, the most numerous, consists of sympatric species but with sporadic hybridizations and generally unviable offspring such as *Aeonium*, *Argyranthemum* Webb and *Sonchus* L.

To advance knowledge of this difficult and complex group of plants, this research project has three main objectives: (1) to continue the chorological study of Voggenreiter (1999) on hybridization in the genera *Aeonium* and *Greenovia* and to validate his results; (2) to synthesize the fundamental principles that govern F1 hybridization in the genera *Aeonium* and *Greenovia* in La Gomera, and to explore if they are fulfilled in the other mountainous islands in the Canary Archipelago; (3) to identify new hybrids in their habitat and to study the particularities in which they occur in nature.

The overall results of this research have been divided into two articles. In the present paper, the results related to the natural history of F1 hybrids and the fundamental principles governing hybridization in the genera *Aeonium* and *Greenovia* are presented. In the second article (Arango 2023c), the taxonomic results are provided, and seven new hybrids discovered in the fieldwork are described and illustrated.

Material and methods

Based on the areas of distribution of the species that make up the genera *Aeonium* and *Greenovia* provided by Voggenreiter (1999), fieldwork was carried out in

many parts of the island of La Gomera. The search for new hybrids was carried out according to the targeted search method developed previously (Arango 2021c). The method consists of three steps: (1) the distribution of all the species in the island was taken from Voggenreiter (1999) and later authors; (2) for each pair of species with overlaps in their areas of distribution, the literature was searched to check whether hybrids between them had been described; (3) for those species pairs that did not have hybrids described, the areas of overlap were extensively searched for potential hybrids.

Data were collected on the morphology, chorology, ecology, and reproductive biology of the taxa that make up both lineages and their hybrids, with special attention to the identification of nothotaxa unknown to science (see Appendix 1). New nothotaxa were recognized by being found living inter parentes and by the distinctive features they presented, according to the critical morphological characters with taxonomic value established by Praeger (1932) and Liu (1989) for the genera *Aeonium* and *Greenovia*.

For the hybridization experiments, cuttings of the different species were grown in the garden until they bloomed. The flowers that were going to act as receptors were emasculated while still in bud stage, and the stigmas covered to prevent unwanted pollination. They were left 24–48 hours for the carpels to become receptive. Pollen from the donor plants was then collected and placed on the stigma. Finally, the pollinated flowers were covered again to prevent further pollinations. After fructification, seeds were collected and planted in the next fall. The seeds were processed and planted according to the technique described by Schulz (2007).

Finally, each of the observational data collected in the field and the laboratory was assigned a score of 0, 1 or 2 (0: the parameter does not exist in the hybrids; 1: it exists but is not constant; 2: it exists and is shared by all natural hybrids), which allowed me to know the common characters in natural hybrids of *Aeonium* and *Greenovia*, and from this information I synthesized the principles governing the phenomenon of hybridization in La Gomera. Then, the analysis of the information stored in the database obtained from the observation of numerous natural hybrids in all the islands and my publications confirm that these principles can be extrapolated to the rest of the mountainous islands of the Canary Archipelago (Arango 2015, 2016a, 2016b, 2017, 2019a, 2019b, 2019c, 2021a, 2021b, 2021c, 2023a).

Results and Discussion

Hybrids in La Gomera

There are 13 taxa of *Aeonium* and *Greenovia* in La Gomera (Fig. 1, Table 1). Therefore, if all could hybridize among them, there would be 78 potential hybrids.

	A. appendiculatum	A. canariense subsp. latifolium	A. castello-paivae	A. decorum	A. decorum var. alucense	A. gomerense	A. holochrysum	A. holochrysum var. rubrolineatum	A. saundersii	A. sedifolium	A. spathulatum	A. lindleyi subsp. viscatum	G. diplocycla
<i>Aeonium appendiculatum</i>													
<i>A. canariense</i> subsp. <i>latifolium</i>	P												
<i>A. castello-paivae</i>	P	D											
<i>A. decorum</i>	D	D	D										
<i>A. decorum</i> var. <i>alucense</i>	X	X	X	P									
<i>A. gomerense</i>	X	P	D	N	X								
<i>A. holochrysum</i>	X	X	P	P	X	X							
<i>A. holochrysum</i> var. <i>rubrolineatum</i>	P	P	P	P	X	X	P						
<i>A. saundersii</i>	P	D	P	N	X	X	X	P					
<i>A. sedifolium</i>	X	X	X	P	P	X	X	X	X				
<i>A. spathulatum</i>	P	P	P	P	X	P	P	D	N	X			
<i>A. lindleyi</i> subsp. <i>viscatum</i>	X	D	D	N	P	P	P	P	P	P	X		
<i>Greenovia diplocycla</i>	P	P	N	D	X	P	P	P	N	X	N	P	

■ = parents sympatric; ■ = parents allopatric; D = hybrids previously described; N = hybrids newly recognized; P = hybrids theoretically possible; X = hybrids not theoretically possible.

Fig. 1. Matrix of all potential crosses among taxa of genera *Aeonium* and *Greenovia* living in La Gomera. For each cross, green background indicates sympatry and, therefore, crossing is theoretically possible, while orange background indicates allopatry and, therefore, crossing is not theoretically possible.

However, as I will argue below, hybridization in nature will only occur when the two parental species coexist in sympatry. Therefore, out of the 78 possible crosses, 27 are not expected to occur due to allopatric distribution of the parents, while 51 potentially exist. Up to now, 10 have been described in the literature and seven additional ones are published in Arango (2023c) (Table 2).
Of the seven new hybrids contributed by Arango (2023c), three are intergeneric between *Aeonium* and

Greenovia. The only representative of the genus *Greenovia* in La Gomera is *G. diplocycla* Webb ex Bolle (Praeger 1929, 1932; Bramwell & Bramwell 2001; Lodé 2010). However, it is a fairly frequent taxon that is distributed throughout almost the entire island and grows intermixed with different species of the genus *Aeonium*. Out of the ten hybrids previously described by other authors, only one was intergeneric, *×Greenonium laxiflorum* J. M. Macarrón & Bañares. The targeted and systematic

search method I have been using favoured the finding of three new intergeneric hybrids of *G. diplocycla* with *A. castello-paivae* Bolle, *A. saundersii* Bolle, and *A. spathulatum* (Hornem.) Praeger (Table 2). Of these, \times *Greenonium cabreræ* A. Santos had already been described in the island of La Palma (Santos 1983). In La Gomera, I found a vicariant nothovariety of the latter in the vicinity of Roque de Ojila, a site where the parents are sympatric.

In a recent study, Messerschmid & al. (2023), in an extensive analysis of the genus *Aeonium* s.l. (including *Greenovia*) concluded that “those islands with the longest history of habitation by *Aeonium* had the lowest percentages of co-occurring and hybridizing taxon pairs compared to islands where *Aeonium* arrived later”. They based this conclusion on their counts of taxa and hybrids in different islands resulting in Gran Canaria (more recently colonized by the genus) having a larger percent of hybrids than Tenerife (colonized earlier). Unfortunately, it appears that these authors finished their sampling in 2019 and have not considered all the novel taxa validly published of the genera *Aeonium* (two species, one subspecies, and ten nothospecies) and *Greenovia* (two species and one nothospecies) since then (Arango 2019a, 2019b, 2019c, 2019d, 2021a, 2023a, 2023b). When all the available data are considered, the numbers of hybrids known in every island are the following: Tenerife 30, La Palma 18, La Gomera 17, Gran Canaria nine and El Hierro six. Moreover, Tenerife (21 taxa and 30 hybrids) has about three times more taxa than Gran Canaria and three times more hybrids (eight taxa vs nine hybrids). Since the number of known hybrids is simply proportional to the number of taxa on an island, the more complex assumption of age of colonization is unnecessary and does not reflect reality.

Experimental crosses

Controlled experiments in the laboratory were essential to understand how F1 hybridization works in the genera *Aeonium* and *Greenovia*. Whenever mature seeds of the new F1 hybrids found in nature were available, a germination test was performed in the laboratory to determine the fertility of the seeds. In addition, to find out if genetic barriers prevented hybridization between species of the genera *Aeonium* and *Greenovia*, different artificial crosses were made between endemic species from different Canary Islands, Madeira, and Cabo Verde (Appendix 2), and all produced fertile seeds and viable embryos. Unfortunately, the two East African taxa, *A. leucoblepharum* Webb ex A. Rich. and *A. stuessyi* H.-Y. Liu, have not flowered in cultivation and similar crosses could not be attempted with Macaronesian species. However, I am not aware of any publication reporting reproductive incompatibility between species of these genera. Therefore, in principle, there are no genetic barriers to hybridization among any species and the seeds of the F1 hybrids are fertile.

Table 1. Total taxa and potential and described hybrids in La Gomera.

Hybrids	Number	Percent
Total number of species and subspecies	13	
Total number of possible crosses (all against all)	78	100
Hybrids not expected due to allopatry	27	34
Hybrids potentially existing due to sympatry	51	65
Described hybrids	17	21
Hybrids described previously	10	13
Hybrids described in Arango (2023c)	7	9

The need for sympatry

As can be seen in Fig. 1, all the described hybrids fulfil the condition that the parental species are sympatric. This can also be seen in Messerschmid & al. (2023: fig. 5). To the best of my knowledge, no hybrid has been described between allopatric species. This can be extrapolated to all the islands. Moreover, this observation appears in most of the descriptions of other authors, in which the comment “found living among the parents” is constantly included. These findings support the hypothesis that parent sympatry is a sine qua non condition for F1 hybridization to occur in the genera *Aeonium* and *Greenovia* in the Canary Islands.). This will constitute the first principle (see below).

One may ask why is sympatry necessary if both pollinating insects and the wind, in principle, seem to have enough capacity to transport pollen to distant places and, as shown in the previous section, there are no barriers to hybridization. Cross-pollination between species of the genera *Aeonium* and *Greenovia* can be carried out by both biotic and abiotic agents, given that most Canary Island plants, including *Aeonium* and *Greenovia*, are considered to have a generalist pollination syndrome. Among the former, insects, lizards, bats and birds have been shown to be active (Bernardello & al. 2001; Olsen & al. 2002; Valido & al. 2004; Esfeld 2009; Padrón & al. 2009; Traveset & al. 2009; Nelson 2010; Severio & Rodríguez-Rodríguez 2011; Ortega-Olivencia & al. 2012; Arango 2013). The wind, in turn, usually only produces the effective dispersal of pollen between individuals located at a short distance (Levin & Kerster 1974). Although some insects can travel several kilometres in their foraging activities and wind can transport pollen over long distances (Heinrich 1979; Roubick 2001; Ollerton & al. 2011), the results of this work show that pollen transfer through these vectors does not work between allopatric species. As mentioned above, all F1 hybrids in La Gomera always occurred when the geographical areas of distribution of the parents coincided (Arango 2023c). This was also the case for the 28 new hybrids studied in other islands of the archipelago (T, GC, P, H) (Arango 2015, 2016a, 2016b, 2017, 2019a, 2019b, 2019c, 2021a, 2021b, 2021c, 2023a).

Table 2. *Aeonium* and *Greenovia* hybrids discovered so far in La Gomera.

Hybrids	Parent 1	Parent 2	Year
Hybrids previously described			
<i>A. ×aguajilvense</i> Bañares	<i>A. castello-paivae</i> Bolle	<i>A. gomerense</i> (Praeger) Praeger	1996
<i>A. ×beltranii</i> Bañares	<i>A. canariense</i> subsp. <i>latifolium</i> (Burchard) Bañares	<i>A. decorum</i> Webb ex Bolle var. <i>decorum</i>	1986
<i>A. ×bravoanum</i> Bramwell & G. D. Rowley ex Heath	<i>A. castello-paivae</i>	<i>A. lindleyi</i> subsp. <i>viscatum</i> (Bolle) Bañares	1992
<i>A. ×castellodecorum</i> Bañares	<i>A. castello-paivae</i>	<i>A. decorum</i> var. <i>decorum</i>	1986
<i>A. ×castelloplanum</i> Bramwell & G. D. Rowley ex Heath	<i>A. canariense</i> subsp. <i>latifolium</i>	<i>A. castello-paivae</i>	1992
<i>A. ×holospathulatum</i> nothovar. <i>sanchezii</i> (Bañares) Bañares	<i>A. arboreum</i> var. <i>rubrolineatum</i> (Svent.) H. Y. Liu	<i>A. spathulatum</i> (Hornem.) Praeger	1996
<i>A. ×perezii</i> Bañares	<i>A. appendiculatum</i> Bañares	<i>A. decorum</i> var. <i>decorum</i>	1990
<i>A. ×sancti-sebastianii</i> Bramwell & G. D. Rowley ex Heath	<i>A. canariense</i> subsp. <i>latifolium</i>	<i>A. saundersii</i> Bolle	1992
<i>A. ×vegamora</i> Bramwell & G. D. Rowley ex Heath	<i>A. canariense</i> subsp. <i>latifolium</i>	<i>A. lindleyi</i> subsp. <i>viscatum</i>	1992
<i>×Greenonium laxiflorum</i> Macarrón & Bañares	<i>A. decorum</i> var. <i>decorum</i>	<i>Greenovia diplocycla</i> Webb ex Bolle	2007
New hybrids (Arango 2023c)			
<i>A. ×dendroides</i> O. Arango	<i>A. decorum</i> var. <i>decorum</i>	<i>A. saundersii</i>	2023
<i>A. ×pendulum</i> O. Arango	<i>A. saundersii</i>	<i>A. spathulatum</i>	2023
<i>A. ×praedictum</i> O. Arango	<i>A. decorum</i> var. <i>decorum</i>	<i>A. gomerense</i>	2023
<i>A. ×rhombifolium</i> O. Arango ⁽¹⁾	<i>A. decorum</i> var. <i>decorum</i>	<i>A. lindleyi</i> subsp. <i>viscatum</i>	2023
<i>×Greenonium cabreræ</i> nothovar. <i>ojilense</i> O. Arango ⁽¹⁾	<i>A. spathulatum</i>	<i>Greenovia diplocycla</i>	2023
<i>×Greenonium haeckelii</i> O. Arango	<i>A. castello-paivae</i>	<i>G. diplocycla</i>	2023
<i>×Greenonium lajense</i> O. Arango	<i>A. saundersii</i>	<i>G. diplocycla</i>	2023

(1) Only the vegetative part is known.

Possibly the large inflorescences of *Aeonium*, formed by numerous brightly coloured flowers, extraordinarily nectariferous and polliniferous, exert an effect of attraction and loyalty to the pollinator, therefore preventing them from having to move to other areas in search of the reward they are looking for (Rademaker & De Jong 1998; Santos & al. 2004; Ares 2019). However, other authors have found low pollen transfer between pairs of sympatric *Aeonium* species and explain their results by a specific behaviour of pollinators during foraging, such as the floral preference of a given species for the reward it receives (Esfeld & al. 2009). They agree with Campbell & al. (2002) that the quality and quantity of pollen transfer are primarily affected by pollinator behaviour rather than variable flower characteristics such as colour, scent, and reward regime.

Finding the missing natural hybrids

The species richness and taxonomic complexity of the genus *Aeonium*, together with its formidable hybridogenic capacity, has generated the largest number of natural hybrids in the entire Canary Island flora, with at least 80 nothotaxa known to date. As mentioned above, there are still many theoretically possible hybrids to be discov-

ered in La Gomera (and in other islands), with at least 34 crosses between species that share the same distribution areas. However, it is becoming increasingly difficult to find new hybrids on the island, possibly due to well-known factors such as (1) the progressive anthropogenization and fragmentation of the natural environment; (2) the serious damage caused by the numerous introduced herbivores (goats and sheep, both domestic and feral) that graze uncontrolled in many parts of the island; (3) the devastating fires that the island has suffered in recent decades; and (4) the negative effects that climate change is causing to the island environment (Caujapé-Castells & al. 2010; Arango 2021d). These factors have led to a critical conservation status (CR) for endemics such as *A. gomerense*, *A. saundersii* and *A. decorum* Webb ex Bolle var. *alucense* (Gómez 1996; Moreno 2008, 2011; IUCN 2012); and if effective solutions are not adopted in the short term, other taxa such as *A. appendiculatum* Bañares, whose distribution area was severely affected by the 2012 fire, probably will have to be added to the list of endangered species.

Generally, recognition of interspecific hybrids in the first filial generation (F1) in the genus *Aeonium* or intergeneric hybrids between *Aeonium* and *Greenovia* is easy, since they are usually found intermixed with the

parents and usually express morphological characters of both. However, determining hybrids in the F2, F3, F4, and successive generations is extremely complex since the characters they express hide inherited traits from the parents. Likewise, the introgressive gene flow caused by backcrossing with the parental species generates progeny with very little morphological differentiation regarding the parents, with which they are generally confused.

Three particular cases illustrate the vagaries of hybrid discovery. An interesting result of this work has been to actually confirm how the distribution areas of two species that originally did not coincide spatially, *Aeonium decorum* var. *decorum* Webb ex Bolle and *A. gomerense* (Praeger) Praeger, have been brought into contact by human action. This has occurred due to the phenomenon that Voggenreiter (1999) called “anthropogenic translocation following the roads” This brought the populations of both parents closer together due to the progressive colonization of the roadside by *A. decorum*; and, as predicted by the German botanist, hybridization between them has eventually occurred. The new nothotaxon, *A. xpraedictum* Arango, was found on one of the edges of the GM-1 road near La Degollada de San Sebastián, the site where the areas of the parents are close to each other. It is a well-known fact that roadsides in the Canary Islands constitute an optimal microhabitat for the propagation of numerous endemism (Delgado & al. 2007; Hengstum 2012).

On the other hand, the cross between *A. decorum* and *A. sedifolium* (Webb ex Bolle) Pithard & Proust, described in Tenerife as *A. xpuberulum* Bañares, has not yet been found in La Gomera. However, it is not ruled out that it may exist in the inaccessible rocky areas of the Puntallana Special Nature Reserve in the east of the island, where both species grow intermingled (Casanova 1990; Voggenreiter 1999). In this case, extremely arid conditions (del Arco & Rodríguez, 2019) may not be favourable for the development of the hybrids, as I have observed that a very high proportion of *Aeonium* seedlings that germinated during the rainy season do not survive very dry and hot summers. At any rate, finding this hybrid in the western part of Tenerife was unexpected, since *A. decorum* is extraordinarily rare in Tenerife (Ceballos & Ortuño 1976; Hernández 1998). Perhaps the environmental conditions of Masca in Tenerife are more favourable to the subsequent development of the progeny.

Finally, in a few cases a hybrid was found away from the parental populations. Usually, the parents were found upwind and/or uphill from the hybrid, suggesting that the seeds were blown away from the parent populations by the wind. The three cases found were *Aeonium xbravoanum* (*A. castello-paivae* × *A. lindleyi* subsp. *viscatum* (Bolle) Bañares in La Gomera; *A. xbornmuelleri* (*A. canariense* subsp. *canariense* (L.) Webb & Berthel. × *A. urbicum* subsp. *urbicum* (C. Sm. ex Hornem.) Webb & Berthel. in Tenerife; *A. canariense* subsp. *canariense* × *A. liui* Arango in Tenerife).

Persistence of the hybrids

Reproduction of natural F1 hybrids by vegetative propagules is rare in *Aeonium* and *Greenovia* and only occurs when the parents are stoloniferous such as *A. simsii* (Sweet) Stearn or *A. cuneatum* Webb & Berthel. In my exhaustive explorations, I have only found two natural hybrids with this property, *A. xstoloniferum* Arango in Gran Canaria and *A. xacebesii* Arango in Tenerife (Arango 2019a, 2021c).

Occasionally, on the five mountainous islands of the Canary archipelago (T, P, G, GC, H), I have found some *Aeonium* forming small hybrid swarms composed of individuals with the ability to reproduce by fertile seeds, possibly obtained by autogamy, backcrossing or introgressive crosses with other species, without ruling out apomixis, which has not been studied in the genus *Aeonium* (Fig. 2). The number of different parental pairs producing these F2 and successive generations does not exceed eight crosses, so they can be considered an exception. Rarer are stable hybrids with the capacity to colonize larger geographical areas, an occurrence which I have only observed on the island of La Palma, where the phenomenon of hybridization is very complex. An example of this type of hybridization can be observed in El Time, a site on the west of La Palma, where it is difficult to find morphologically representative specimens of *A. davidbramwellii* H. Y. Liu, and most of the population is composed of hybrid specimens. Probably, this population has reached stability by successive backcrosses with the parental species or by introgressive crosses with other species with which it shares its distribution area. This phenomenon is well known in other taxonomically complex groups such as *Biscutella* L. (*Cruciferae*). Some authors have chosen to consider these stabilized hybrids as species of hybridogenic origin in the absence of data that would place them definitively in the nothospecies rank (Mateo 2023).

Principles governing hybridization in the genera *Aeonium* and *Greenovia*

Analysis of the results of this work and those of Voggenreiter (1999), plus studies of numerous natural hybrids on other mountainous islands of the archipelago (GC, H, P, T), and methodical observations (Arango 2015, 2016a, 2016b, 2017, 2019a, 2019b, 2019c, 2021a, 2021b, 2021c, 2023a) have provided essential information to better understand the natural history of F1 hybrids of the genera *Aeonium* and *Greenovia*, which I have synthesized into the following eight principles. The principles governing hybridization in the F1 generation in the genera *Aeonium* and *Greenovia* have been expressed as principles and not as laws because, in natural sciences, laws are universal, while principles are subject to biological evolution and changes in the natural environment and may have exceptions (Elgin 2003; Martínez & al. 2017).



Fig. 2. Seedbed of a hybrid swarm of *Aeonium* \times *junoniae* Bramwell & G. D. Rowley ex Heath from La Palma, obtained with seeds from nature, which confirms occasional fertility of some hybrids in F2 generation or later.

First principle — F1 hybridization in nature only occurs between species that share the same geographic area, or at least where the areas of distribution of both parents come into contact at some point. Pollen transfer through biotic and abiotic agents does not work between disjunct areas.

Second principle — When two species that share the same geographical area have overlapping blooming phenology, F1 hybridization always ends up occurring between them.

Third principle — Crosses between the different species produce fertile seeds that give rise to F1 hybrids since there are no genetic barriers between them to prevent this. However, the fertility of F1 hybrids is quite variable, ranging from absolute sterility to complete fertility.

Fourth principle — Seeds of F1 hybrids usually germinate where they originate, but given their small size they are, in rare cases, dispersed by the wind and germinate between hundreds of meters and a few kilometres away from the site where they were formed.

Fifth principle — The evolutionary aptitude of F1 hybrids in nature, understood as the capacity to survive or reproduce successfully, is usually low or null, and they generally disappear from the natural environment in the F1 generation. However, some crosses do generate fertile hybrids with a certain stability and ability to form small swarms, but they are the exception.

Sixth principle — The number of hybrid individuals generated by the different crosses in nature does not depend on the size of the populations of the parental species or on the taxonomic affinity between them, such as belonging to the same section or to the same molecular clade. The most common is that they occur in a low frequency.

Seventh principle — Generally, F1 hybrids express the morphological characters inherited from both parents in similar proportions. But in some cases, the alleles of one parent are dominant over those of the other, making the offspring more closely resemble the dominant parent.

Eighth principle — Despite the low fertility of the F1 hybrids, back-crossings of these with the parental species occur in nature sporadically. When this occurs, it produces genic introgression and morphological convergence between the progeny and the parents.

From these principles, it can be deduced that the only two effective prezygotic barriers that prevent intraspecific F1 hybridization in the genus *Aeonium* and intergeneric hybridization between *Aeonium* and *Greenovia* in the Canary Islands are the geographical separation of the populations and the different flowering times. Probably, the time they have been separated has not been long enough to establish such reproductive barriers. Moreover, the efficacy of different flowering times as a reproductive barrier is decreasing due to climate change effects in the Canary Islands. Nowadays, it is increasingly common to observe earlier flowering, lengthening of the flowering period or extemporaneous flowering (unpublished data of the author). This fact is evident when comparing the phenological data I have collected since 2010 with the flowering dates provided by Liu (1989), many of them obtained from historical herbarium sheets. These changes in floral phenology will make the appearance of new natural hybrids possible.

Final comments

Although individual hybrids in the genera *Aeonium* and *Greenovia* usually disappear from nature in the first filial generation, they can produce gene dilution in the species with which they coexist, as pollen viability can reach 80–90% in some hybrids (Liu 1989). Hence the importance of recognizing hybrids in nature, describing them, and depositing the types in herbarium collections. In addition, they should be included in all Canary databases, as is done by the website Endémicas Canarias (2023), because they can contribute to a better understanding of the evolutionary history and phylogeny of the flora of the Canary Islands.

A better understanding of the chorology, ecology, and reproductive biology of the genera *Aeonium* and *Greenovia* may favour the development of new conservation strategies to ensure the long-term survival of these plants. Increasingly, importance is being given to the detrimental effects of hybrids on the species due to the loss of genetic identity, which compromises their reproduction and makes them more vulnerable to various threats in the natural environment. It is also well known that genes, evolution, and environmental adaptation always go together (Levin & al. 1996; Francisco-Ortega & al. 2000; Brilhante & al. 2021). Perhaps understanding these phenomena can help to explain why the Canary

Island Network of Protected Natural Spaces (Law 12/1994 of 19 December 1994), after three decades of operation, has failed to protect *Aeonium* species, which are in a critical state of conservation category CR (IUCN 2012), since they are all found within protected areas, and none have recovered, neither in number of individuals nor in area covered. It would be interesting to find out why these areas have not achieved such a basic objective as in situ conservation of threatened species (Chape & al. 2005; Reyes-Betancort & al. 2008; Moreno 2015; IUCN 2012).

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Appendix 1

Additional material studied — SPAIN, CANARY ISLANDS, LA GOMERA: *Aeonium xaguajilvense* Bañares (*A. castello-paivae* Bolle × *A. gomerense* (Praeger) Praeger), Aguajilva, 700 m, May 1991, Á. Bañares (TFC 37963). *Aeonium xbeltrani* Bañares (*A. canariense* subsp.

Appendix 2

Experimental crosses between allopatric species of *Aeonium* and *Greenovia*. All crosses resulted in fertile seeds and viable embryos. – (CV) = Cabo Verde; (G) = La Gomera; (GC) = Gran Canaria; (H) = El Hierro; (L) = Lanzarote; (M) = Madeira; (T) = Tenerife.

Parent 1	Parent 2
Inter archipelagos	
<i>A. arboreum</i> (L.) Webb & Berthel. subsp. <i>arboreum</i> (GC)	<i>A. glutinosum</i> (Aiton) Webb & Berthel. (M)
<i>A. arboreum</i> subsp. <i>arboreum</i> (GC)	<i>A. gorgoneum</i> J. A. Schmidt (CV)
<i>A. glandulosum</i> Webb & Berthel. (M)	<i>A. urbicum</i> (C. Sm. ex Hornem.) Webb & Berthel. subsp. <i>urbicum</i> (T)
<i>A. glutinosum</i> (M)	<i>A. haworthii</i> Salm-Dyck ex Webb & Berthel. (T)
<i>A. glutinosum</i> (M)	<i>A. sedifolium</i> (Webb ex Bolle) Pit. & Proust (G)
<i>A. glutinosum</i> (M)	<i>A. tabuliforme</i> (Haw.) Webb & Berthel. (T)
<i>A. gorgoneum</i> (CV)	<i>A. haworthii</i> (T)
Inter islands	
<i>A. canariense</i> (L.) Webb & Berthel. subsp. <i>canariense</i> (P)	<i>A. simsii</i> (Sweet) Stearn (GC)
<i>A. canariense</i> subsp. <i>christii</i> (Burchard) Bañares (P)	<i>A. pseudourbicum</i> Bañares (T)
<i>A. canariense</i> subsp. <i>christii</i> (P)	<i>G. millennium</i> O. Arango (T)
<i>A. davidbramwellii</i> H. Y. Liu (P)	<i>A. lancerottense</i> (Praeger) Praeger (L)
<i>A. davidbramwellii</i> (P)	<i>A. liui</i> O. Arango (T)
<i>A. decorum</i> Webb ex Bolle var. <i>decorum</i> (G)	<i>A. haworthii</i> (T)
<i>A. decorum</i> var. <i>decorum</i> (G)	<i>A. simsii</i> (GC)
<i>A. goochiae</i> Webb & Berthel. (P)	<i>A. volkeri</i> E. Hern. & Bañares (T)
<i>A. haworthii</i> (T)	<i>A. nobile</i> (Praeger) Praeger (P)
<i>A. lindleyi</i> subsp. <i>viscatum</i> (Bolle) Bañares (G) ⁽¹⁾	<i>A. nobile</i> (P)
<i>A. liui</i> (T)	<i>A. percarneum</i> (R. P. Murray) Pit. & Proust (GC)
<i>A. mascaense</i> Bramwell (T)	<i>A. sedifolium</i> (G)
<i>A. mascaense</i> (T)	<i>A. simsii</i> (GC)
<i>A. pseudourbicum</i> (T) ⁽¹⁾	<i>A. saundersii</i> Bolle (G)
<i>A. pseudourbicum</i> (T)	<i>A. simsii</i> (GC)
<i>A. saundersii</i> (G)	<i>A. simsii</i> (GC)
<i>A. sedifolium</i> (G)	<i>A. simsii</i> (GC)
Intra islands	
<i>A. arboreum</i> var. <i>holochrysum</i> H. Y. Liu (H)	<i>A. valverdense</i> (Praeger) Praeger (H)
<i>A. canariense</i> subsp. <i>christii</i> (P)	<i>A. spathulatum</i> (Hornem.) Praeger (P)
<i>A. haworthii</i> (T)	<i>A. smithii</i> (Sims) Webb & Berthel. (T)
<i>A. holochrysum</i> var. <i>rubrolineatum</i> (Svent.) H. Y. Liu (G) ⁽¹⁾	<i>A. lindleyi</i> subsp. <i>viscatum</i> (G)
<i>A. mascaense</i> (T)	<i>A. pseudourbicum</i> (T)
<i>A. mascaense</i> (T)	<i>G. aurea</i> (C. Sm. ex Hornem.) Webb & Berthel. (T)

(1) Hybrid created by Carles Jiménez Box.

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