

Checklist of the *Cistus* hybrids occurring in Southern Portugal

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Abstract. Southwest Portugal is rich in *Cistus* species and its hybrids. A global review of all sixteen *Cistus* nothotaxa found in Southern Portugal is provided with a nomenclatural update and the typification of previous described nothotaxa (*Cistus* × *daveaunus*). A new hybrid is described (*C.* × *aljezurensis* nothosp. nov.) relating the introgression between *C. crispus* and *C. inflatus*.

Keywords: *Cistaceae*, hybridization, nothospecies, Aljezur, Algarve, Portugal.

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Introduction

The *Cistaceae* family (*Malvales*) has eight genera, with ca. 180 species and is one of the most characteristic and abundant in the Mediterranean Region. It occupies numerous habitats, and its flowering and characters are typically adapted to the prevailing xeric ecological conditions (Fernández-Mazuecos & Vargas, 2018). After more than 40 years since Pinto da Silva's (1980) publication, we provide an overview of the actual knowledge about *Cistus* species and its hybrids in the Southwest of Portugal.

The genus *Cistus* is subdivided into three subgenera. Subgenus *Cistus* L. includes all pink flowering species. Subgenus *Leucocistus* includes most white flowered species, except *C. libanotis*, which is separated into the third subgenus *Halimionides*. *Cistus libanotis* occurs on the South Coast of Portugal and South of Lisbon, but not in the Southwest of Portugal. In Portugal, no hybrids are known from this species. There are two pink flowering *Cistus* species occurring in southwestern Portugal: *C. albidus* and *C. crispus*, while four species possess white flowers: *C. inflatus*, *C. ladanifer*, *C. monspeliensis*, *C. populifolius* subsp. *major* and *C. salviifolius*.

Lamarck (1786) described *C. inflatus* under the name of *C. hirsutus* as a previous name already used for another species. Forty years later, Robert Sweet called the species *C. psilosepalus*, valid until Jean-Pierre Demoly identified Sweet's type as *C.* × *laxus* Aiton (1997), a hybrid between this species and *C. populifolius*. Demoly recovered *C. inflatus* as it was used by Pierre André Pourret, for this species. The investigation of *Cistus* hybrids in Portugal started with Jules Daveau in 1886 when he published "*Les Cistinées du Portugal*". Later on, a list of *Cistus* hybrids that pretty much corresponds to today's knowledge

was published by A.R. Pinto da Silva in "*Os híbridos de Cistus em Portugal*", in 1980. Although plant hybrids are under-recorded by botanists (Preston & Pearman, 2015), Southwest Portugal is particularly rich in hybrids of *Cistus*. Demoly (1996) considered 27 of the 37 reported binary hybrids, across natural and artificial combinations that are usually sterile.

Dansereau (1938) was the first to indicate that *Cistus* species frequently give homoploid hybrids, referring to Anderson's studies focusing on introgressive plant populations (Anderson 1949). Homoploid hybrids are hybrids between two species that have the same number of chromosomes (Rieseberg & Willis, 2007). In homoploid speciation, the hybrids growing naturally in mixed populations are not characterized by genome duplication and isolation must develop through other mechanisms (Rieseberg & Willis, 2007). Since Anderson's studies on homoploid hybrid populations of Louisiana irises are known, these populations occur in hybrid zones created by disturbances and ecotones. The existence of these novel niches allows for the persistence of hybrid lineages (Harrison & Rand, 1989).

As Talavera *et al.* (1992) illustrated for *C. ladanifer*, fecundity is highly dependent on nearest neighbor distance, with isolated plants often setting no fruit, whereas plants within a clump set fruit in nearly all flowers. Based on this observation, we conclude that the close neighborhood of different *Cistus* species is the *conditio sine qua non*, for the presence of hybrids. In 2005, Demoly & Montserrat (2005) added some hybrids to their chapter about *Cistus* in Flora Iberica without any description or indication of distribution. For example, in the Monchiquense District (Vila-Viçosa & Arsénio, 2021), it is quite common to find pure stands of the hybrid between *C. populifolius* and *C. salviifolius* (*Cistus* × *hybridus* Pourr.). Or,

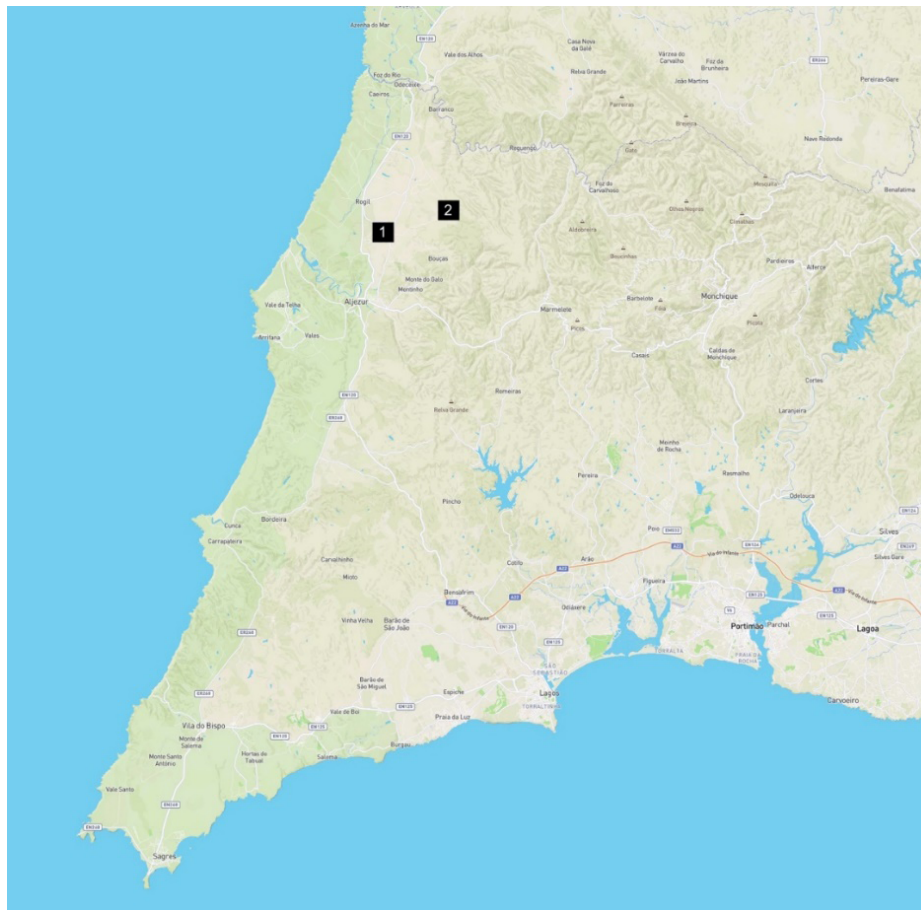


Figure 1. Study area in southern Portugal (Algarve).

near streams above schists where the soil texture becomes harder clay, it is common to observe the transition of *C. ladanifer* dominated communities to *C. monspeliensis* dominated communities in hard clay soils. Here is where the hybrids are common. (Lousã *et al.*, 1989).

The Iberian flora exhibits seventeen taxa inside the genus *Cistus* L. (*Cistaceae*) (Demoly & Montserrat, 1993). Twelve were designated at the specific rank, with seven subspecific entities, in addition to 70 proposed nothotaxa (Demoly & Montserrat, 1993). Hybridization within this genus is a very frequent phenomenon in nature, which seems to constitute an active mechanism of speciation within this plant group (Guzmán & Vargas, 2005).

The degradation of climax forests from historical times, combined with the abandonment of cultivated land in the last 40 years, led to the establishment of pioneer communities of *Cistus*, namely *Cistus salviifolius*, *C. ladanifer* and *C. inflatus* (Costa *et al.*, 2012), which are quite adapted to cycling anthropic fires, in comparison to the natural forest or cultivated land. The effect of cyclic fires in the Portuguese Southwest works as a permanent restart of the ecological successional dynamics, maintaining these pioneer scrublands above eroded and shallow soils. In this type of scrubland, gorse-heathlands and rockrose communities are the dominant type of vegetation, which respectively corresponds to *Calluno-Ulicetea* and *Cisto-Lavanduletea* classes, while *Cistus inflatus* is a representative of the *Ericion umbellatae* alliance (Costa *et al.*, 2012; Vila-Viçosa & Arsénio, 2021).

The main objective of this article is to provide an overview and checklist of all *Cistus* hybrids occurring in Southwest Portugal, including the correspondent nomenclatural update and description of a new unreported hybrid.

Material and Methods

Study area

The Southwest of Portugal is dominated by siliceous bedrock, which results in poor acidic soils (Kopp, 1989), often dystric cambisols or ferric podzols. These result in a mosaic of secondary scrubland vegetation of *Lavanduletea stoechadis* (*Cisto-Lavanduletea*) and heathlands of *Ericenion umbellatae* (*Calluno vulgaris-Ulicetea minoris*). Around the village of Aljezur, there are some places where relicts of carbonated soil resisted erosion, such as small patches on the widespread geological residual Paleozoic areas.

Fieldwork was taken from February to May of 2020 and 2021. Additionally, seed samples were collected in September of the same year.

We selected two areas (see map) for a closer assessment of *Cistus* species and their hybrids (Figure 1):

1. Carrascalinho (37.351866–8.781150°)

West of the houses of the little village of Carrascalinho, North from Aljezur, Algarve, Portugal, about 60 m asl, is thriving an isolated population of *Cistus albidus* on a relict spot of marine Tertiary carbonated soils. The place is enclosed in areas of acidic bedrock of Carbon slate, unappropriated



Figure 1. Example of contrasting flowers belonging to *C. albidus* (left) and *C. x daveauanus* (right) through blue tinted sunglasses revealing the color differences.

for *Cistus albidus* but where *Cistus inflatus* is quite common, above oligotrophic and sandy soils.

2. Brejo Longo (37.361303–8.743775°)
Brejo Longo is situated on Pleistocene and Quaternary sand deposits about 7,5 km northeast of Aljezur, about 200 m asl. Here the typical habitat with sub-mesophyllous scrubland vegetation of *C. inflatus* of Atlantic influence (Guzmán *et al.*, 2009) forms often a mosaic with a Mediterranean scrubland where sub-heliophyllous species like *C. ladanifer* and *C. salviifolius* dominate (Guzmán *et al.*, 2009).
The detection of hybrids in the field was based on intermediate leaf and flower patterns, presented by hybrids, mostly in stands of one or both parent species. In some cases, the overlap of flowering periods led to the presence of hybrids. An example is *C. x incanus* with thick clusters of pink flowers, easily diagnosed when *C. crispus*, the dominant

species in the area, also possesses pink flowers but is not flowering. Blue-tinted sunglasses were used to detect *C. x daveauanus* in a fully flowering stand of *C. albidus* (Figure 1). The authors took pictures of all parts of the plants and samples. All *Cistus* taxa and nothotaxa were registered and photographed, specimens were collected for herbarium deposit at Oporto University (PO) and further studies.

Results and Discussion

We report six species of the Genus *Cistus* in the Portuguese Southwest. The taxa found at Carrascalinho (6 species and 4 nothospecies) and its abundance are presented in Table 1. The diverse microhabitat complexity may explain the high number of *Cistus* taxa and nothotaxa in the Brejo Longo area, as shown in Table 2.

Table 1. List of *Cistus* taxa, corresponding to six species and four nothospecies, registered around Carrascalinho, North of Aljezur, Southwest Portugal, and its abundance. Abbreviations are: + very rare, max. 2 specimens found per season; ++ rare, 2-5 specimens found per season; +++ not rare, 5-10 specimen found per season; ++++ common, >10 specimens found per season.

| | <i>C. albidus</i> | <i>C. crispus</i> | <i>C. monspeliensis</i> | <i>C. inflatus</i> | <i>C. salviifolius</i> | <i>C. ladanifer</i> |
|-------------------------|------------------------|-------------------|--------------------------|--------------------|------------------------|---------------------|
| <i>C. albidus</i> | ++++ | ++ | | ++ | | |
| <i>C. crispus</i> | <i>C. x incanus</i> | + | | | | |
| <i>C. monspeliensis</i> | | | ++++ | | + | + |
| <i>C. inflatus</i> | <i>C. x daveauanus</i> | | | | | |
| <i>C. salviifolius</i> | | | <i>C. x florentinus</i> | | + | |
| <i>C. ladanifer</i> | | | <i>C. x stenophyllus</i> | | | +++ |

Table 2. List of *Cistus* taxa (6 species and 12 nothospecies) registered at Brejo Longo, Aljezur, Southwest Portugal. Abbreviations are: + very rare, max. 2 specimens found per season; ++ rare, 2-5 specimens found per season; +++ not rare, 5-10 specimens found per season; ++++ common, >10 specimens found per season.

| | <i>C. crispus</i> | <i>C. monspeliensis</i> | <i>C. populifolius</i> subsp. <i>major</i> | <i>C. inflatus</i> | <i>C. salviifolius</i> | <i>C. ladanifer</i> subsp. <i>ladanifer</i> |
|---|---|--------------------------|---|--------------------------|------------------------|--|
| <i>C. crispus</i> | ++++ | | | + | ++ | + |
| <i>C. monspeliensis</i> | | + | + | ++ | | ++ |
| <i>C. populifolius</i> subsp. <i>major</i> | | <i>C. × longifolius</i> | ++ | ++ | ++ | ++ |
| <i>C. inflatus</i> | <i>C. × aljezurensis</i> nothosp. nov. | <i>C. × platysepalus</i> | <i>C. × laxus</i> | ++++ | ++++ | +++ |
| <i>C. salviifolius</i> | <i>C. × novus</i> | | <i>C. × hybridus</i> | <i>C. × obtusifolius</i> | ++++ | ++ |
| <i>C. ladanifer</i> | <i>C. × fernandesae</i> | <i>C. × stenophyllus</i> | <i>C. × aguilari</i> | <i>C. × dansereau</i> | <i>C. × verguinii</i> | ++++ |

Description of the hybrids

The following description of the occurrence and abundance of *Cistus* hybrids is based on personal observations over more than 10 years in SW Portugal. Several visits were made with regular weekly prospections in the reference areas during the flowering period from January to June. Table 3 lists the *Cistus* hybrids from Southwest Portugal.

Species across the genus *Cistus* are often inter-fertile and hybridized in nature. Hybrids of species of the same subgenus are more frequent, and

the progeny are often fertile. Hybrids of species between subgenera *Cistus* and *Leucocistus* are less common and sterile. Depending on which of the two species is the pollen-donor or receiver parent, hybridization events between different species can produce quite distinct progeny. Often, traits of both parent species can be found in all parts of the plant (leaves, indumentum, bracts, flowers). Closed flower buds and bracts can be good traits for comparing taxa in the field (Figure 2). The red dot line shows the limit between the subgenus *Cistus* (above) and *Leucocistus* (below).

Table 3. *Cistus* hybrids from Southwest Portugal.

| Hybrid name | Origin species |
|--|--|
| <i>Cistus × aljezurensis</i> New, see this publication | <i>C. crispus</i> × <i>C. inflatus</i> |
| <i>Cistus × aguilari</i> O.E.Warb. J. Roy. Hort. Soc. 56: 222 (1931) | <i>C. ladanifer</i> × <i>C. populifolius</i> subsp. <i>major</i> |
| <i>Cistus × dansereau</i> P. Silva Agron. Lusit. 40: 22 (1980) | <i>C. ladanifer</i> × <i>C. inflatus</i> |
| <i>Cistus × daveaunus</i> P. Silva Agron. Lusit. 40(1): 20 (1980) | <i>C. albidus</i> × <i>C. inflatus</i> |
| <i>Cistus × fernandesae</i> P. Silva in Agron. Lusit. 40: 21 (1981) | <i>C. ladanifer</i> × <i>C. crispus</i> |
| <i>Cistus × florentinus</i> Lam. Encycl. 2: 17 (1786) | <i>C. monspeliensis</i> × <i>C. salviifolius</i> |
| <i>Cistus × hybridus</i> Pourr. Mém. Acad. Sci. Toulouse 3: 312 (1788) | <i>C. populifolius</i> subsp. <i>major</i> × <i>C. salviifolius</i> |
| <i>Cistus × incanus</i> L. Sp. Pl.: 524 (1753) | <i>C. albidus</i> × <i>C. crispus</i> |
| <i>Cistus × laxus</i> Aiton Hort. Kew. 2: 233 (1789) | <i>C. populifolius</i> subsp. <i>major</i> × <i>C. inflatus</i> |
| <i>Cistus × longifolius</i> Lam. Encycl. 2: 16 (1786) | <i>C. populifolius</i> subsp. <i>major</i> × <i>C. monspeliensis</i> |
| <i>Cistus × obtusifolius</i> Sweet Cistineae: t. 42 (1827) | <i>C. inflatus</i> × <i>C. salviifolius</i> |
| <i>Cistus × platysepalus</i> Sweet Cistineae: t. 47 (1827) | <i>C. monspeliensis</i> × <i>C. inflatus</i> |
| <i>Cistus × stenophyllus</i> Link Enum. Hort. Berol. Alt. 2: 74 (1822) | <i>C. ladanifer</i> × <i>C. monspeliensis</i> |
| <i>Cistus × verguinii</i> Coste Bull. Soc. Bot. France 55: 475 (1908) | <i>C. ladanifer</i> × <i>C. salviifolius</i> |
| <i>Cistus × lecomtei</i> Sennen Monde Pl. 32: 24 (1931) | <i>C. albidus</i> × <i>C. monspeliensis</i> |
| <i>Cistus × rodiaei</i> Verg. Bull. Soc. Bot. France 79(4): 600 (1932) | <i>C. albidus</i> × <i>C. ladanifer</i> |
| <i>Cistus × albeerensis</i> Gaut. ex Rouy & Foucaud Fl. France 2: 268 (1895) | <i>C. albidus</i> × <i>C. salviifolius</i> |

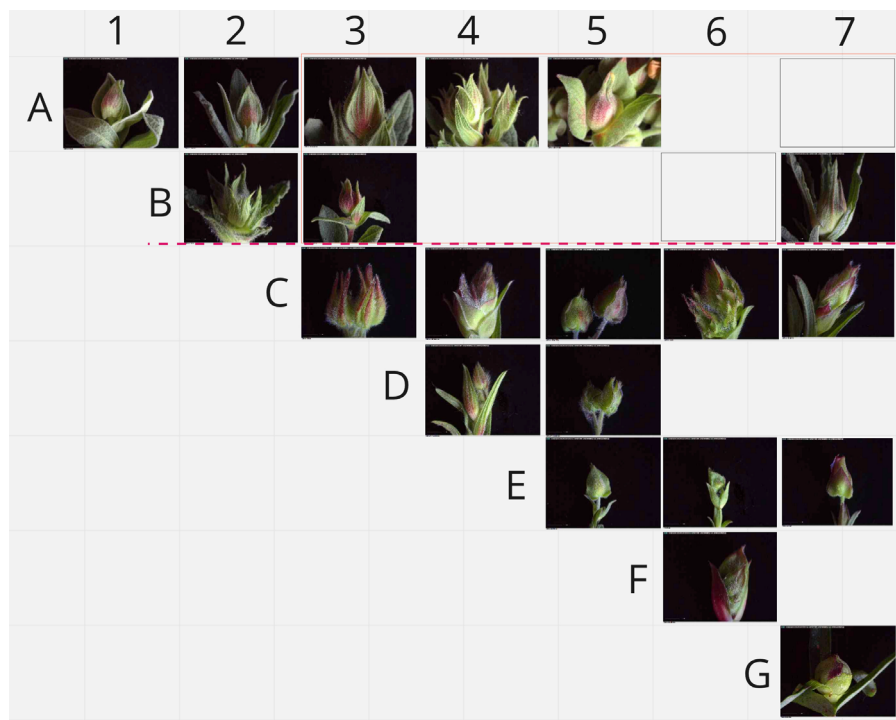


Figure 2. Bracts of *Cistus* species and its hybrids in the Southwest of Portugal. A1, *C. albidus*; A2, *C. × incanus*; A3, *C. × daveaunus*; A4, *C. × lecomtei*; A5, *C. × albeerensis*; B2, *C. crispus*; B3, *C. × aljezurensis*; B7, *C. × fernandesae*; C3, *C. inflatus*; C4, *C. × platysepalus*; C5, *C. × obtusifolius*; C6, *× laxus*; C7, *× dansereau*; D4, *C. monspeliensis*; D5, *C. × florentinus*; E5, *C. salviifolius*; E6, *C. × hybridus*; E7, *C. × verguinii*; F6, *C. populifolius* subsp. *major*; G7, *C. ladanifer*.

***Cistus × aljezurensis* U. Schwarzer & C. Schwarzer nothosp. nov.** (Figures 3, 4)

Parent species: *Cistus crispus* × *C. inflatus*

Very rare. It is not an abundant hybrid, found in only a few individuals (in total 3). Flowering time is quite late, only 5 weeks from the midst of April to the end of May. Flowering peak from the end of April to the end of May. Some flowers, at the same time, are flowering quite well.

Holotype: Portugal, Algarve, Aljezur, Brejo Longo, 37.3622, -8.7410, 181 m asl, 31/III/2020, Leg.: U. Schwarzer & C. Schwarzer (PO-V69769), Figure 3. **Isotype:** (LISE 96317).

Description: Small bush up to 55 cm, procumbent to upright, glanduliferous and hirsute. Leaves (15)20 × 40 mm, sessile to fused, oval lanceolate to oblong, some slightly undulate, often twisted in the apex, revolute, upper leaves green to greyish, lower and older leaves often yellowish with 3–5 nerves, the external often incomplete, with stellate hairs.

Tip of the leaf pointed. The inflorescence is composed of 3 or more flowers on the tip and two laterals with longer peduncles (5–10 mm), with bracts persistent covering the calyx. Sepals (8)10–15(18) mm, cordiform and ciliated, green to yellow when young, older becoming dark purple. Petals 18–19 (25) × 20–25 mm, purple to pale purple, wrinkled. Uneven stamens, longer than their pistil. Seeds are about 1,2 mm, rounded to triangular, often depressed in the center, and have a brown rugose surface.

It differs from *C. crispus* in the non-wrinkled leaves and an indumentum with a higher number of trichomes. It differs from *C. inflatus* by the presence of stellate trichomes and the pink color of its flowers. Seeds of

C. × aljezurensis are produced very sparsely, often malformed, and are smaller than those of *C. crispus*, and lack the dark brown color of those from *C. inflatus*. Notes: Hybrid plants come from the natural crossing between *C. crispus* and *C. inflatus*; they differ from *C. crispus* in the flat leaves and are not wrinkled. It differs from *C. inflatus* by the pink color of its flowers. Seed production is very sparse. If existing, they are intermediate between the two parentals. The seeds are smaller and do not have the brown dark color of *C. inflatus*, and they are bigger than the ones from *C. crispus*.

Etymology: Dedicated to the nearby town of Aljezur.

In April 2020, the authors found three specimens flowering at the edge of *Cisto-Lavanduletalia* communities close to a public tar road. They, apparently, did not belong to one of the known species occurring locally. Guzmán & Vargas (2005) indicated that field-identification of *Cistus* hybrids is relatively easy since they display intermediate characters between both putative parents. In autumn (2020), only two specimens of this spontaneous hybrid could be found living in nature.

C. inflatus and *C. crispus* are considered parapatric species (Demoly, 1996). This is revealed to be inaccurate, as the hybrid is clearly recognized by its intermediate features and the detection of sympatric sub-populations in Southern Portugal. The assumption made by Demoly (1996) may arise from the fact that both parentals belong to different subgenera, inside the genus *Cistus* (Ellul, 2002). *C. crispus* belongs to subgenus *Cistus* and *C. inflatus* to the subgenus *Leucocistus*. But hybrids between species of different subgenera are known from the genus *Cistus* and two of them also occur in the study areas: *C. × fernandesae* and *C. × novus* (see Table 2).



Figure 3. Holotype of *Cistus x aljezurensis*.



Figure 4. Flowering *Cistus x aljezurensis* U. Schwarzer & C. Schwarzer, nothosp. nov. (PO-V69769), 11.4.2020, Brejo longo, Aljezur.

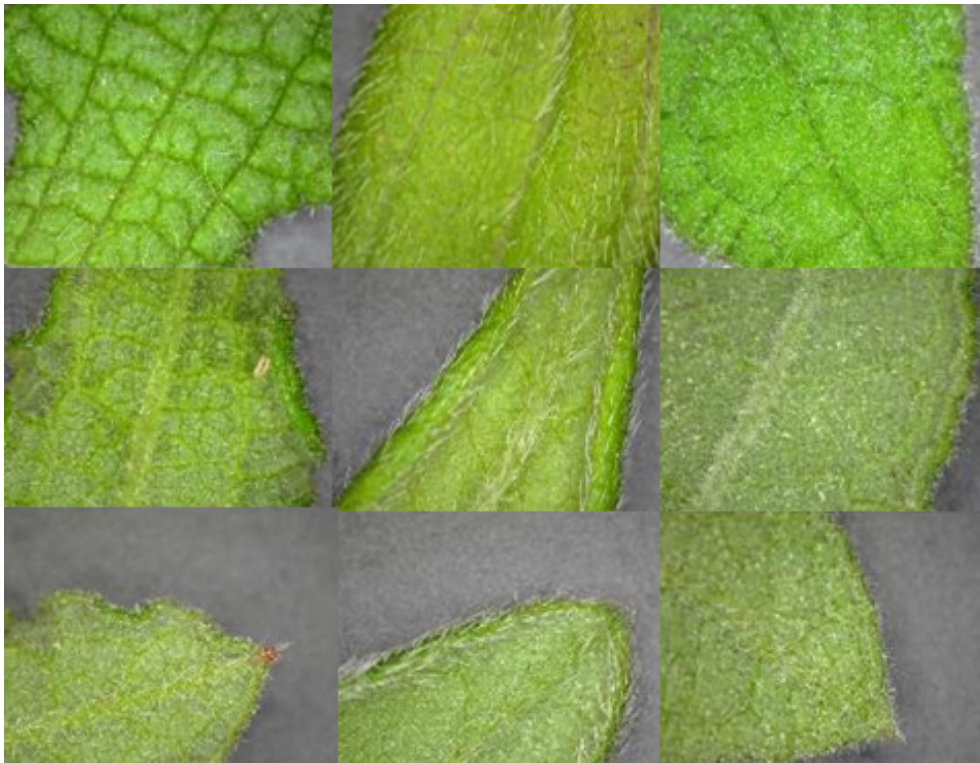


Figure 5. Leaves, from left to right, of *C. crispus*, *C. inflatus* and *C. x aljezurensis*.
From up to bottom, the adaxial view, the abaxial view and leaf tips.

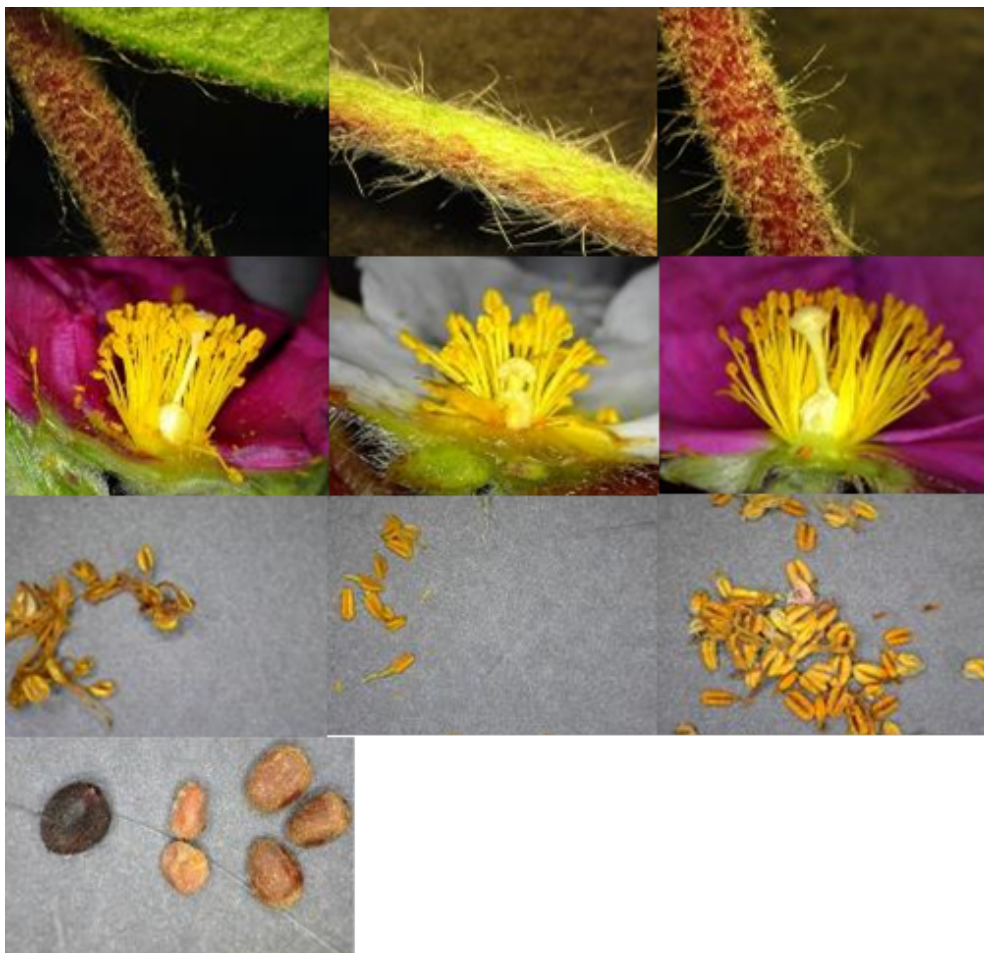


Figure 6. From left to right, flowers of *C. crispus*, *C. inflatus* and *C. x aljezurensis*.
From up to bottom, peduncles, sections of flowers, anthers and seeds.

Table 3. Main differential characters between *C. nothosp. aljezurensis* and its parentals.

| | <i>Cistus crispus</i> | <i>Cistus inflatus</i> | <i>Cistus</i> × <i>aljezurensis</i> |
|-----------------------|--|--|--|
| Habit | Shrub 20-50 (70) cm, dense, procumbent branches, aromatic, of an intense green color and very scaly, reddish-brown and shiny bark; Twigs, with stellate hairs and simple hairs, unicellular, long, very white, and multicellular glanduliferous. | Shrub 60-100 (120) cm, erect, tall, very branchy, pubescent when young, with short glandular hairs and other simple, long hairs – up to 2 mm –, patent and inserted in a basal tubercle. | Small bush up to 55 cm, procumbent to upright, glanduliferous hirsute. |
| Leaves (Figure 5) | Leaves 12-35 × 4-13 mm, sessile – welded at the base in a reddish sheath, very short –, ovate or elliptical to ovate-lanceolate or lanceolate and even linear-lanceolate, wavy-frizzy margin and 3- 5 nerves. The adults have a dark green upper surface, very rough, with stellate hairs, plus some simple unicellular and multicellular glanduliferous hairs, and paler reticulate underside, with stellate hairs and multicellular glanduliferous hairs. Leave tip mucronate. | Leaves 30-65 × 10-23 mm, oval-lanceolate or oblong, flat or slightly revolute, trinerved, accentuated, of an intense green color, with simple hairs scattered on the upper surface and starlets on the underside; petiole inconspicuous, flat. Leave tip obtuse. | Leaves (15)20 × 40 mm, sessile to welded, oval lanceolate to oblong, some slightly undulate, most twisted at the tip, revolute, upper leaves green to greyish-green, lower, older leaves often yellowish, 3-5 nerves, the outer often not complete with star hairs. Leave tip pointed. |
| Inflorescence | Inflorescence short, contracted at the dense top of short pedicels (1-5 mm), and covered by persistent bracts that hide the calyces. | Inflorescence pauciflora or multiflora, cymoid, sometimes partially subscorpioid; pedicels 5-14 mm, long, with non-involved bracts and drooping bracts. | Inflorescence composed by 3 or more on the tip and two laterals with longer peduncles flowers, pedicels 5-10 mm, bracts persistent covering the calyx. |
| Sepals | Sepals 5, 11-20 × 3-8 mm, persistent, ovate-acuminate to ovate-lanceolate ± acuminate, densely covered with stellate hairs, simple unicellular hairs and some glanduliferous multicellular hairs. | Sepals 5, all similar, hirsute and long ciliated, with twisted margins; the external ones, 13-25 × 8-14 mm, larger, cordiform, yellowish-green or at the end purple. | Sepals (8)10-15(18) mm, cordiform and ciliate, green to yellow when young, older dark purple. |
| Petals | Petals 12-20 × 10-20 mm, stout, striated, with a slightly frizzy margin, of an intense purple color, sometimes pink, rarely albino. Subequal stamens. | Petals 14-22 × 10-18 mm, ivory-white, with yellow basal spot. Uneven stamens, longer than its pistil. | 18-19 (25) × 20-25 mm, purple to pale purple, wrinkled. Uneven stamens, longer than their pistil. |
| Ovaries (Figure 6) | Sericeous-vile ovary; filiform style, barely surpassed by the stamens; stigma convex, slightly pentalobulated. Capsule 5-6 mm, ovate-oblong, subglabrous, loculicidal in 5 valves. | Ovary densely sericeous-tomentose; short style – c. 0.5 mm –; stigma large, crenulate. Capsule 5-6 mm, included in the calyx acrid, ovoid, somewhat pubescent, blackish, dehiscent in 5 valves. | Ovary densely tomentose; long style; stigma large, hemisphere. Capsule < 5 mm, ovoid, subglabrous, brown, dehiscent in 5 valves. |
| Seed (Figure 6) | Seeds c. 1 mm, smooth head, light brown. | Seeds 1,2-1,5 mm in diameter, globose, slightly foveolate, dark in color. | Seeds about 1,2 mm, round to triangular, rugose surface, brown. |

Cistus* × *aguilari Pau in Mem. Real Soc. Esp. Hist. Nat., Tomo Extr.: 290 (1921) (Figure 7)
= *C. x aguilari* var. *longifolius* Font Quer in Bol. Soc. Esp. Hist. Nat. 25: 175 (1925)

Parent species: *Cistus ladanifer* × *Cistus populifolius* subsp. *major*

Notes: In the area, this rare hybrid is not abundant, with only a few specimens present. Its flowering period falls quite late, spanning merely three weeks from mid-April to early May, with the peak of flowering occurring towards the end of April. At any given time, only a few flowers are in bloom, characterized by an inflorescence with an asymmetrical cyme. The flower buds exhibit a range from light green to reddish hues, with external sepals featuring mucronate to cuspidate tips and densely covered with glands. These flowers are of medium size, white in color, adorned with prominent dark blotches. The plant bears sessile lanceolate leaves with entire margins, occasionally

Figure 7. *C. x aguilari*

ciliate or colored, and while somewhat sticky, they exhibit less stickiness compared to *C. ladanifer*. The

venation pattern is cross-venulate, with small veins connecting the secondary veins. Branches of the plant are typically brown-reddish in color.

Cistus × dansereau P. Silva in Agron. Lusit. 40: 22 (1980) (Figure 8)

= *C. × lusitanicus* Maund. Bot. Gard.: 7, tab. 649 (1837), pro sp., nom illeg., non Mill. (1768)

Parent species: *Cistus ladanifer* × *Cistus inflatus*

Notes: This abundant hybrid is frequently found, with several plants reliably appearing yearly. Its flowering period extends for over 15 weeks, spanning from the middle of March to the middle of June, with the peak bloom occurring from early April to late May. The plant boasts multiple flowers simultaneously, displaying a robust flowering performance. Its inflorescence forms in terminal symmetrical cymes, with flower buds ranging from light green to dark red, particularly noticeable in the revolute margins of the bracts, which are often hairy. The medium-sized white flowers each feature a small reddish, feathered basal blotch on every petal. Its sessile linear leaves are elongated with slightly undulated margins, exhibiting a sticky texture, albeit less so compared to *C. ladanifer*. Longitudinal venation characterizes the leaves, with veins predominantly aligned along the leaf axis. The branches of this hybrid typically display shades of brownish-red.



Figure 8. *C. × dansereau*

Cistus × daveauanus P. Silva in Agron. Lusit. 40(1): 20 (1980) (Figures 9–12)

Parent species: *Cistus albidus* × *Cistus inflatus*

Notes: This very rare hybrid has only been recorded once since 1886, and until now, it has been found in only a few specimens. Its flowering period is relatively lengthy, spanning seven weeks from the beginning of April to the end of May, with the peak bloom occurring from the end of April to the middle of May. The inflorescence forms in terminal asymmetrical cymes, often producing twin flowers. The closed flower buds match the green hue of the leaves, with external sepals adorned with short and long hair and veins tinged with reddish tones. Several pink flowers typically bloom simultaneously, showcasing a robust flowering performance. The sessile, silvery grey-green leaves are hairy, lanceolate or elliptic in shape, and exhibit varying degrees of reticulate-rugose

texture, with smaller veins forming a network-like pattern.

In 1913 Pereira Coutinho had included in his “Flora de Portugal” a short description of the hybrid of “*C. albidus* × *hirsutus* (Dav.)” indicating peduncles and calix as “tomentose and long villous”, leaves “lanceolate or elliptic, more or less reticulate-rugose”. In 1980 Pinto da Silva named a hybrid *Cistus × daveauanus*, which Daveau in 1886 has described as *Cistus hirsutus* × *albidus* based on a single plant from Portugal. *Cistus hirsutus* is a non-valid name of *Cistus inflatus*. The findings of Daveau and the description of Pinto da Silva have been so far the only available indication that this hybrid exists in nature until the authors found specimens near Aljezur in 2020.

The review of the original literature and solely available specimens of *C. × daveauanus* leads to the need for lectotypification. Pereira Coutinho (1913) includes in his “Flora de Portugal” a description of “*C. albidus* × *hirsutus* (Dav.)” but does not mention that he has the only voucher collected by Jules Daveau in June 1882. In the study on the *Cystaceans* that Jules Daveau published in the Bulletin of the Broterian Society, vol. IV, 1886 is referred to the specimen of A.R. da Cunha. Pinto da Silva, in 1980, gave the hybrid a name: *Cistus × daveauanus* (in Pinto da Silva, A.R. 1980: *Cistus* hybrids in Portugal. Agron. Lusit. 40(1): 19–26).

In a *Phlomidio purpureae*-*Cistetum albidae* above eroded limestone with *Cistus albidus* and *Cistus monspeliensis* near the village of Carrascalinho, North of Aljezur, we discovered three individuals of *Cistus × daveauanus* (see Table 1), while only one specimen of *Cistus crispus* was found in the surrounding area. No other *Cistus* species were present within the population, neither *Cistus inflatus*.

The hybrid was easily separated from *C. albidus* by its flowering characteristics, that contrast in form, size and color (see habitat, Figure 9). While *Cistus albidus* has more purple flowers, all flowers of *C. × daveauanus* show pink flowers (Figure 10). Notable were as well the revolute edges of the sepals (Figure 10). In autumn, *C. albidus* plants were very often found covered with empty fruit capsules, while the hybrid exemplars had only very few dry inflorescences, often not matured, and with the sepals still holding the capsule. The average length of *C. albidus* capsules was 8 mm, while those of *C. × daveauanus* was 5 mm (Figure 10).

Due to these characteristics and the close vicinity of *C. inflatus* populations *C. × daveauanus* presence was confirmed in the Carrascalinho sub-population of *C. albidus* and *C. monspeliensis*. It is the first time that this hybrid was referenced in Portugal, after Daveau’s discovery in 1886. An individual has been collected by the authors (PO-V 70069), and comparisons were established with the parental *C. albidus* (Figure 11). *C. × daveauanus* is distinguishable by the sepals with revolute edges and lanceolate oval, tomentose whitish leaves, flat and distinctly trinerved. Pereira Coutinho description of leaves (1913) confirms “lanceolate or elliptic, more or less reticulate-rugose” leaves of this hybrid (see Figure 11). The choice of the lectotype (LISU 2564P; Figure 12) was based on the careful examination of available specimens and published descriptions and follows the guidelines of the Shenzhen Code (Turland *et al.*, 2018).



Figure 9. Habitat portrait in Carrascalinho site with *Cistus albidus* (foreground and left) and *Cistus* × *daveauanus* (above, right side).



Figure 10. Differences in flower characteristics between *Cistus* × *daveauanus* and *C. albidus*. A, purple flower of *C. albidus* (left), pink flower of *C. x daveauanus* (right); B, revolute edges of the sepals, as major distinctive character of *Cistus* × *daveauanus*; C, capsules of *C. albidus* (left) and *C. x daveauanus* (right), with notorious canescent trichomes in the hybrid, while being pannose in the parental.

Cistus* × *fernandesae P. Silva in Agron. Lusit. 40: 21 (1981) (Figure 13)
= *C. x fontii* Sennen in Bol. Soc. Aragonesa Ci. Nat. 15: 224 (1916), nom. nud.

Parent species: *Cistus ladanifer* ssp. *ladanifer* × *Cistus crispus*

Notes: This hybrid is very rare, often appearing as a single specimen only in certain years. Its flowering period is relatively short, lasting four weeks from the end of April to the end of May, with the peak bloom occurring in the middle of May. Multiple flowers usually

bloom simultaneously, displaying a robust flowering performance. The flowers are pale pink, of medium size, adorned with red dots, characteristic of the variety *maculatus*. The variety *imaculatus* is even rarer, usually appearing as a single specimen only. Its flowering period is even shorter, lasting three weeks from the end of April to the beginning of May, with the peak bloom occurring in early May. The inflorescence forms in terminal cymes, often solitary or in pairs. Closed flower buds of the variety *imaculatus* are glossy and vivid green, hairy, with cuspidate bracts tipped in red. Only a few flowers typically bloom simultaneously,



Figure 11. Comparison of *C. albidus* (left column) and *C. x daveauanus* (right column). From up to bottom, flower, bracts and sepals; indumentum on abaxial sides of leaves; vein structures on abaxial sides of leaves; hair types of young twigs.

but they are showy and wrinkled, vivid pink, and comparatively large. The sessile linear leaves are elongated, with a blue-greyish hue due to the hairy surface, featuring ciliate and entire, slightly undulated margins. Venation is parallel, with secondary veins creating a network pattern more pronounced towards the leaf tip. The leaves are sticky, but to a lesser extent than *C. ladanifer*. Dark brown branches complete the plant's appearance.

Cistus x florentinus Lam. Encycl. 2: 17(1786), pro sp. (Figure 14)
 = *C. x varius* Pourr. in Hist. & Mém. Acad. Roy. Sci. Toulouse 3: 312 (1788) pro sp.
 = *C. x florentinus* var. *apriciformis* Rouy & Foucard, Fl. France 2: 270 (1995)
 = *C. x florentinus* var. *grandiflorus* Sennen & Pau in Bol. Soc. Aragonesa Ci. Nat. 11: 183 (1912)

Parent species: *Cistus monspeliensis* × *C. salviifolius*

Notes: This hybrid is rare, typically appearing as single specimens only, producing numerous flowers. Flowering observation from early April until beginning



Figure 13. *C. x fernandesae*

of May. Its inflorescence forms in terminal scorpioid cymes. Closed flower buds are vivid green and hairy, with narrow brown margins that later develop reddish-tinged veins. The small white flowers have petals ranging from triangular to heart-shaped. The sessile leaves are vivid green, twisted, lanceolate



Figure 12. *Cistus* × *daveauanus* Pinto da Silva Agron. Lusit. 40(1):19–26 (1980). Lectotype: LISU2564P.

to ovate in shape, and hairy, with undulate margins adorned with cilia. Venation is parallel at the base, fanning out towards the leaf tip, with secondary veins forming a network pattern. Branches of this hybrid typically exhibit a greenish hue.



Figure 14. *C. x florentinus*

***Cistus* × *hybridus* Pau (Figure 15)**

= *C. x hybridus* nothosubsp. *grandiflorus* (Pau) M.B. Crespo & Mateo in Collect. Bot. (Barcelona) 18: 96 (1990)
 = *Cistus* × *corbariensis* nothovar. *grandiflorus* Pau in Actas Soc. Esp. Hist.-Nat. 1899: 90 (1899).
 = *Cistus* × *corbariensis* nothovar. *australis* Font Quer in Cavaanillesia 1: 34 (1928).



Figure 15. *C. x hybridus*.

Parent species: *Cistus populifolius* subsp. *major* × *Cistus salviifolius*.

Notes: This hybrid is rare, typically found in only a few specimens. Its flowering period is very short, spanning just two weeks from the end of April to the beginning of May. It produces only a few flowers at a time. The inflorescence forms in terminal cymes, often solitary. Closed flower buds are green, cordate, and hairy, with narrow reddish margins, while older bracts transition from light green to reddish-brown. The flowers themselves are white and of medium size. The shortly petiolate leaves are lanceolate, slightly twisted, hirsute

leaves with slightly undulated, entire, ciliate margins. Old leaves are of dark green color, with a smooth topside and a rough bottom side. Young leaves are vivid green, soft and hirsute. There is a longitudinal venation on the leave base, turning reticulate towards leaf tips. Old branches are of a reddish color, whereas young branches are green and hirsute.

Cistus × incanus L. Sp. Pl.: 524 (1753), pro sp. (Figure 16)

= *C. polymorphus* f. *incanus* (L.) Batt. in Battandier, J.A. & Trabut, L.C. Fl. Algérie, Dicot.: 88 (1888), nom. illeg.

= *C. vulgaris* var. *incanus* (L.) Steud. in Nomencl. Bot., ed. 2, 1: 375 (1840), nom. superfl.

= *C. × dellei* Burnat in Fl. Alpes Marit. 1: 163 (1892)

= *C. × incanus* f. *albiflorus* Delip. & Cheshm. in God. Sofiisk. Univ. "Kliment Okhridski" Biol. Fak. 2, Bot. 88(4): 74 (1997)

= *C. × pulverulentus* Pourr. in Mém. Acad. Sci. Toulouse 3: 312 (1788)

Parent species: *Cistus albidus* × *C. crispus*

Notes: This hybrid is locally present, typically manifesting in a few specimens only but with longer persistence. Its flowering period is remarkably extended, commencing on warm days in December or January and persisting until June. The peak flowering season spans 15 weeks from the beginning of March to the end of June, with the highest bloom density occurring from April to May. Its inflorescence forms in terminal symmetrical cymes, often producing twin flowers. Closed flower buds ovate, matching the green hue of the leaves, and are hairy and ciliate, with acuminate bracts exhibiting purple veins that later turn reddish. Numerous flowers bloom simultaneously, displaying a strikingly intense magenta pink color that surpasses that of the parental species. The sessile lanceolate to elliptic leaves are silvery green, grey to blueish in color, somewhat twisted, and hairy, with undulate margins. Venation is parallel, with secondary veins creating a network pattern. The branches of this hybrid are dark reddish-brown in hue.



Figure 16. *C. × incanus*

Cistus × laxus Aiton Hort. Kew. 2: 233(1789), pro sp. (Figure 17)

= *C. × hirsutus* var. *nigrescens* Merino in Mem. Real Soc. Esp. Hist. Nat. 2: 511 (1904)

= *C. × nigrescens* (Merino) Font Quer in Bol. Soc. Esp. Hist. Nat. 25: 174 (1942)

= *C. × laxus* var. *nigrescens* (Merino) P. Silva in Agron. Lusit. 10: 101 (1948)

= *C. × merinoi* Pau in Bol. Soc. Aragonesa Ci. Nat. 3: 263 (1904)

= *C. × subhirsutus* Rothm. in Bol. Soc. Esp. Hist. Nat. 34: 153 (1942)

= *C. × laxus* f. *pedroi* P. Silva in Agron. Lusit. 10: 101 (1948), nom. nud.

= *C. × laxus* f. *subhirsutus* (Rothm.) P. Silva

Parent species: *Cistus populifolius* subsp. *major* × *Cistus inflatus*

Notes: This hybrid is rare, typically found in only single specimens. Its flowering period is very short, lasting just two weeks from the end of April to the beginning of May. It produces only a few flowers at a time. The inflorescence forms solitary flowers in terminal cymes. Closed flower buds are green, slightly revolute, and cuspidate, with a hairy and ciliate texture, while older bracts turn reddish-brown. The flowers themselves are white and of medium size. The leaves are sessile, vivid green, lanceolate, and very hairy, with older leaves transitioning to a greyish-dark green hue. They exhibit a pinnate venation with a network pattern of smaller veins towards the leaf tip, while the venation at the leaf base shows a longitudinal vein's structure. Branches are bi-colored, green and reddish.



Figure 17. *C. × laxus*

Cistus × longifolius Lam. in Encycl. 2: 16 (1786) (Figure 18)

= *Cistus × nigricans* Pourr. in Mém. Acad. Sci. Toulouse 3: 311 (1788)

= *Cistus × longifolius* var. *grosii* Font Quer in Cavanillesia 1: 33 (1925)

= *Cistus × longifolius* subsp. *grosii* (Font Quer) Demoly, P.Monts., Muñoz Garm. & C.Navarro in Fl. Iber. 3: 336 (1993)

= *Cistus × nigricans* subsp. *grosii* (Font Quer) M.B.Crespo & Mateo in Collect. Bot. (Barcelona) 18: 97 (1990)

= *Cistus × nigricans* var. *grosii* (Font Quer) Demoly in Biocosme Mésogéen 18: 152 (2002)

= *Cistus × nigricans* var. *longifolius* (Lam.) M.B.Crespo & Mateo in Collect. Bot. (Barcelona) 18: 97 (1990)

Parent species: *Cistus populifolius* subsp. *major* × *C. monspeliensis*

Notes: This hybrid is very rare, typically emerging as single specimens only. There have been no flowering indications reported for 2022. Its inflorescence forms in terminal cymes, often appearing as solitary flowers or in pairs. Closed flower buds are green with reddish glands and a red tip. The flowers themselves are white and of medium size. The leaves are sessile, narrow lanceolate, and dark green, with a lighter green shade on the abaxial side. They possess a sticky surface, similar to that of *C. ladanifer*. Venation is mainly longitudinal. The branches of this hybrid are brown in color.



Figure 18. *C. × longifolius*

Cistus × obtusifolius Sweet in Cistineae: tab. 42 (1827), pro sp. (Figure 19)

Parent species: *Cistus inflatus* × *C. salviifolius*

Notes: This hybrid is very abundant, frequently seen year after year. In places where it occurs, one can find numerous plants every year, making it even more common than the original species. Its flowering period is exceptionally extended, spanning over twelve weeks from the middle of March to the end of May, with the peak bloom occurring from April to May. This hybrid is very floriferous, with an abundance of flowers blooming simultaneously, and they last a long time. Its inflorescence forms in terminal cymes, often appearing as solitary flowers. Closed flower buds are cordate and vivid green, with reddish narrow margins, while older bracts transition from green to reddish-brown, and are ciliate and hairy. The flowers themselves are white and of medium size, with triangular petals. The leaves are sessile, fresh green, slightly hairy, lanceolate, with ciliate and undulate margins. Venation is parallel, with smaller veins forming a network pattern. The branches of this hybrid are green.

Cistus × platysepalus Sweet in Cistineae: tab. 42 (1827), pro sp. (Figure 20)

Parent species: *Cistus monspeliensis* × *C. inflatus*

Notes: This hybrid is very rare, typically only appearing as a single specimen. Its flowering period is remarkably extended, lasting for more than twelve weeks from the beginning of March to the beginning



Figure 19. *Cistus × obtusifolius*

of June, with a particularly long peak bloom from the end of March to the end of May. It is overwhelmed with numerous flowers blooming simultaneously, creating a strikingly floriferous appearance that seems to have more flowers than leaves. Its inflorescence forms in terminal cymes, often presenting as solitary or twin flowers. Closed flower buds are vivid green with a hirsute central vein and ciliate texture, while older bracts turn more yellow to reddish-brown and become hairy. The flowers themselves are white, slightly wrinkled, with huge, strongly overlapping petals. The sessile leaves are lanceolate to linear, small and very narrow, with a glossy green surface and ciliate revolute margins. Venation is mainly longitudinal at the base, becoming arcuate towards the tip, where smaller veins form a network pattern. The branches of this hybrid are reddish to brown in color.



Figure 20. *Cistus × platysepalus*.

Cistus × stenophyllus Link (Figure 21)

= *C. ladanifer* var. *stenophyllus* (Link) Grosser in H.G.A.Engler (Ed.). Pflanzenr., IV, 193: 24 (1903)

= *C. × loretii* Rouy & Foucaud in Fl. France 2: 279 (1895)

= *C. × loretii* var. *albiflorus* Rouy & Foucaud in Fl. France 2: 279 (1895)

= *C. × loretii* var. *maculatus* Rouy & Foucaud in Fl. France 2: 279 (1895)

= *C. lusitanicus* var. *decumbens* Maund in Bot. Gard. 9: 799 (1841)

- = *C. × stenophyllus* f. *albiflorus* (Rouy & Foucaud) Demoly in Biocosme Mésogéen 11(2): 30 (1994)
- = *C. × stenophyllus* f. *concolor* Demoly in Biocosme Mésogéen 18: 155 (2002)
- = *C. × stenophyllus* var. *grandifolius* Demoly in Biocosme Mésogéen 18: 155 (2002)
- = *C. × stenophyllus* f. *guttatus* Demoly in Biocosme Mésogéen 18: 155 (2002)

Parent species: *Cistus ladanifer* × *C. monspeliensis*
 Notes: This hybrid is highly uncommon, usually manifesting as single specimens only. Its flowering period is short, lasting for four weeks from the beginning to the end of April. It produces only a few flowers at a time, typically appearing solitary in terminal cymes. Closed flower buds are glossy and vivid green with dark purple veins, and they are ciliate. As they age, bracts become more yellow with dark purple veins and tips, also exhibiting a ciliate texture. The small white flowers have small dark red to black feathered basal blotches on each petal. The sessile leaves range from vivid to dark green, linear, and glossy, with ciliate margins. They are slightly sticky but less so than *C. ladanifer*. Venation is parallel, with secondary veins creating a network pattern. The branches of this hybrid are brown in color.



Figure 21. *Cistus × stenophyllus*

Cistus × verguinii Coste in Bull. Soc. Bot. France 55: 475 (1908) (Figure 22)
 = *C. × verguinii* f. *albiflorus* Demoly in Biocosme Mésogéen 11(2): 30 (1994)

Parent species: *Cistus ladanifer* × *C. salviifolius*
 Notes: This hybrid is rare, not commonly found in the area, usually present in only a few specimens. Its flowering period is relatively late, spanning only four weeks from the beginning of April to the beginning

of May. There's no distinct flowering peak observed. It produces few flowers at a time, typically appearing solitary in terminal cymes. Closed flower buds are cordate and glandular, reddish towards the tip, with older bracts turning red. The small flowers have huge maroon blotches at the base of each petal, giving the impression that the blotches nearly touch those on the adjacent petals. The leaves are shortly petiolate, lanceolate to linear, with entire margins, often brown in color, and slightly sticky, though much less so than *C. ladanifer*. Venation is cross-venulate. The branches of this hybrid range from reddish to brown in color.



Figure 22. *Cistus × verguinii*

Hybrids from South Coast of the Eastern Algarve, Portugal



Figure 23. *Cistus × albeerensis*

Cistus × albeerensis Gaut. ex Rouy & Foucaud (Figure 23)
 = *Cistus × gautieri* Rouy & Foucaud, Fl. France 2: 268 (1895)

Parent species: *C. albidus* × *C. salviifolius*

Notes: This hybrid is rare, typically only appearing as single specimens. Its flowering period occurs in April. The inflorescence forms in terminal symmetric cymes, often with solitary flowers. Closed flower buds match the color of the leaves, being grey-green, hirsute, ovate, with a slightly reflected acuminate tip. As they age, the bracts develop lightly purple-colored veins. The flowers themselves are pink with wrinkled petals. The leaves are sessile, ranging from linear to ovate in shape, green-grey in color, and hirsute, sometimes with crenate, revolute margins. Venation is parallel, with secondary veins creating a network pattern. The branches of this hybrid are hirsute and light brown in color.

Cistus* × *lecomtei Sennen Monde Pl. 32(190): 24 (1931) (Figure 24)

Parent species: *Cistus albidus* × *C. monspeliensis*

Notes: This hybrid is rare, typically only appearing as single specimens. There is no indication of the flowering time for 2023. It produces some flowers at the same time, often with solitary flowering in terminal symmetric cymes. Closed flower buds match the color of the leaves, being grey-green, hirsute, ovate, with a slightly reflected acuminate tip. Older bracts develop lightly purple-colored veins. The flowers are small and very pale pink. The leaves are sessile, ranging from lanceolate to linear in shape, green-grey in color, and hirsute, with entire margins that are slightly revolute. Venation is parallel, with secondary veins creating a network pattern. The branches of this hybrid are greenish to light brown.



Figure 24. *Cistus* × *lecomtei*

Cistus* × *rodiaei Verg. (Figure 25)

= *C. × purpureus* Lam. in Encycl. 2: 14 (1786)

= *C. × purpureus* f. *argenteus* Demoly in Bull. Soc. Bot. Centre-Ouest n.s. 16: 93 (1985), no Latin descr.

= *C. × purpureus* var. *argenteus* Demoly in Bull. Soc. Bot. Centre-Ouest n.s. 16: 93 (1985)

= *C. × purpureus* f. *holorhodos* Demoly in Biocosme Mésogéen 14: 117 (1998)

= *C. × purpureus* f. *stictus* Demoly in Bull. Soc. Bot. Centre-Ouest n.s. 16: 93 (1985)

Parent species: *Cistus ladanifer* × *C. albidus*

Notes: This hybrid is generally very rare, typically only manifesting as single specimens over the

years. Its flowering period occurs from April to May. It produces numerous flowers at the same time, displaying a robust flowering performance. The inflorescence forms in terminal cymes, often with solitary flowering. Closed flower buds are light green, hirsute, acuminate, with a reddish tip, while older bracts develop some reddish veins. The flowers themselves are comparatively large, purple, pink, with a chocolate colored basal blotch on the base of each petal. The sessile leaves are lanceolate to elliptic and broad, ranging in color from green to blueish-grey, and are hirsute with a corrugated surface and undulate margins. They are slightly sticky, but much less so than *C. ladanifer*. Venation is cross-venulate. The branches of this hybrid are brownish in color.



Figure 25. *Cistus* × *rodiaei*

Final remarks on *Cistus* hybrids

With a total of seventeen nothotaxa, the Portuguese Southwest presents itself as a very rich area for *Cistus* hybrids. It includes all the eight species occurring in Algarve and towards the Spanish border, where nearly all possible combinations of parent species can be found.

Demoly (1996) has shown that subgenera and sections are good guides to the potential hybridization and the fertility of the resulting offspring. While hybrids of the same subgenus are often frequent in nature, when in sympatry and the progeny are commonly fertile. The same author considered that the barriers for hybridization



Figure 26. Comparison of fading in dried *Cistus* petals. Left, fresh preparation; right, preparation after 1 year. Left column (from up to bottom): *C. x aljezurensis*, *C. x incanus*, *C. albidus*. Right column (from up to bottom): *C. inflatus*, *C. crispus*, *C. x daveauanus*.

between species of different subgenera, *Cistus* and *Leucocistus*, are rather genetic than mechanic. But the presence in nature of *C. x fernandesae*, *C. x aljezurensis*, *C. x daveauanus*, *C. x lecomtei* and *C. x albeerensis* (the last one, *C. albidus x salviifolius*, not yet found in SW Iberian Peninsula) shows that the barriers for hybridization are not very tight and can be mostly limited by the sympatry of parent species. The special geological and ecological conditions in the Algarve, mainly in the Mediterranean-Atlantic Southwest, allow overlapping populations and thus the occurrence of an elevated number of rare *Cistus*-hybrids. Important is also the relationship of *Cistus* hybrids to their parents. At least one parent species is always occurring in spatial context with the hybrid.

Cistus species have a naturally hybridogenous nature, but some hybrids are more often found in nature. Especially *Cistus ladanifer* and *C. inflatus* hybridize easily. In this context one must take into consideration that subgenus *Leucocistus* has more species, so there are more possibilities for hybridization in this subgenus. All hybrids with white flowers in SW Portugal belong to this group. The group of subgenus *Cistus* is smaller, in SW Portugal with only two species: *C. albidus* and *C. crispus* and only one common hybrid: *C. x incanus*.

Hybrids between species from the different subgenera *Cistus* and *Leucocistus* are extremely rare and are often reduced to single plants and scattered in time (only in some years) like *C. fernandesae*, *C. purpureus*, *C. lecomtei* and *C. x albeerensis*. The new nothospecies described in this article (*C. x aljezurensis*), and *C. x daveauanus*, which was only known from one single exemplar found in Portugal in 1886 belong to this group as well. All those hybrids between species of different subgenera have parents which are known for their promiscuous nature, like *C. ladanifer*, *C. monspeliensis* and *C. inflatus*. They do produce most of the hybrids in SW Portugal. As shown in Table 4, *Cistus ladanifer* and *C. monspeliensis* are involved in six *Cistus* hybrids, hybridizing with all other species available in the area. As well *Cistus inflatus* is involved in six *Cistus* hybrids, including the new described hybrid *C. x aljezurensis* and the rediscovered *C. x daveauanus*. Three nothospecies which Demoly considered as “one or two specimens found in nature” and “non sympatric

species” are present in the Portuguese Southwest (*C. x fernandesae*, *C. x daveauanus*, and *C. x aljezurensis* nothosp. nov.) are documented in detail in this article.

Table 4. List of number of hybrids per *Cistus* species.

| Species | N. hybrids |
|--|------------|
| <i>C. albidus</i> | 5 |
| <i>C. crispus</i> | 4 |
| <i>C. inflatus</i> | 6 |
| <i>C. ladanifer</i> | 6 |
| <i>C. monspeliensis</i> | 6 |
| <i>C. populifolius</i> subsp. <i>major</i> | 4 |
| <i>C. salviifolius</i> | 5 |

Regarding the hybrid *C. x daveauanus*, Demoly (1996) examination of the lectotype, conserved in Lisbon (LISU) confirms the presence of a thick tomentum of stellate trichomes on younger twigs and in the underside of the leaves and the sepals. He has no doubt about the parentage, referring in *schedullae*: “*C. psilosepalus* (*C. hirsutus*)” can be recognized by “sepals with revolute edges” and *C. albidus* with “sessile, lanceolate oval, tomentose whitish leaves as well as the whole plant”. Although small (4-7 x 14-25 mm), the leaves are flat and distinctly trinerved.

The key given by Demoly includes the hybrid in the species group with white flowers. Given the fact that Pereira Coutinho had only the voucher specimen (LISU) collect by Jules Daveau in June 1882, it is not surprising that the pink color has had disappeared by the time.

In our own experience, the flower color disappears, without further treatment, in dry *Cistus* specimen within a few months (Figure 26).

Checking the overlap known in the distribution in Portugal of *Cistus albidus* and *Cistus inflatus* (Figure 27) we could approximate the distribution of *C. x daveauanus* in those overlapped areas indicated in red. Comparing the typus locality for *C. x daveauanus* with the study locality, they share to be on the boundary of the larger distribution patches of *Cistus albidus*. The first (orange grid in the map of Figure 27) is the typical location for *Rhamno laderoi-Quercetum*

rotundifolia in Mamedano district that contacts with the granite areas of *Arisaro-Quercetum pyrenaica* with understorey of *Halimio-Cistetum psilosepali*. The second (blue grid) in the most Northern area of the Algarve population of *Cistus albidus* with *Phlomidopurpureae-Cistetum albidum* on eroded soils derived from limestones relict remnants close to acidic heathland of the *Ericion umbellatae* with *Cistus inflatus*.

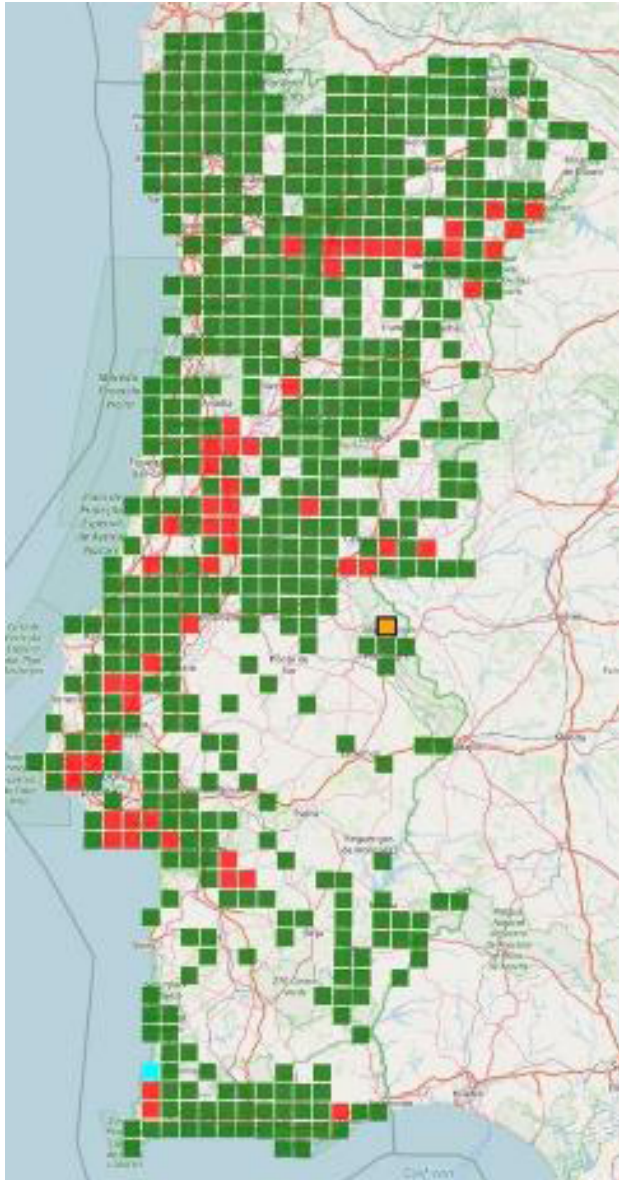


Figure 27. Map showing the distribution in Portugal of *C. inflatus*, in green and the overlap with *C. albidus* in red (Porto et al., 2021). The orange grid square indicates Covões near Marvão (typus locality for *Cistus × daveauanus*). The blue grid square indicates Carrascalinho in the Northwestern Algarve, where these nothospecies was recently found.

Most of the hybrids are showing intermediate features between both parents' species, regarding leaves and flowers and are usually easy to recognize. The flowers, especially colored ones, are very helpful in detecting and distinguishing these hybrids. Hybrids of *Cistus ladanifer* show blotches with their own characteristics in color and form.

In the flowering period, some *Cistus* hybrids are easily detected in the field. Examples are *Cistus × obtusifolius* and *C. × dansereau*, with *Cistus*

inflatus as one parent species in both. Hybrids with *Cistus crispus* as one parent species are difficult to spot because they are very rare, such as *C. × aljezurensis*, *C. × daveauanus*, *C. × fernandesae* (both, *forma maculatus* and *forma immaculatus*). As well, hybrids with *C. monspeliensis* are quite rare, like *C. × florentinus*, *C. × longifolius*, *C. × platyphyllus* and *C. × stenophyllus*. All those rare hybrids can be found only as single plants, while the more common hybrids appear in large groups or mixed within the stands of at least one of their parent species.

Regarding their flowering period, *Cistus* hybrids behave quite differently. Some have an extremely short flowering time of two weeks only, all where *C. populifolius* subsp. *major* is involved: *C. × aguilar*, *C. × hybridus* and *C. × laxus*. The reason might be the flowering behavior of the mentioned parent species. From all species known from the SW of Portugal, *C. populifolius* has the shortest flowering period. On the contrary, hybrids where *C. inflatus* is enrolled with a remarkable flowering period of 17 weeks like *C. × dansereau*, *C. × obtusifolius* and *C. × platysepalus* of almost 15 weeks.

The flowering patterns presented by all *Cistus* species and hybrids across the springtime of 2022 are shown in Table 5. The flower season of different *Cistus* species vary from year to year, especially in temperature and, intensity and duration of rainy periods.

Regarding *C. × aljezurensis*, the flowering times of the parental species *C. crispus* and *C. inflatus* are well synchronized. It is evident that *C. inflatus* is one of the first flowering in March while *C. crispus* has its most flower development from the second half of April onwards until the end of May. *C. × daveauanus*, the hybrid of *C. albidus* and *C. inflatus*, is assumed to be quite rare due to asynchronous flowering times. Statistical data of flowering time for both species in Portugal (www.flora-on.pt, accessed on April 22, 2022) show that *C. albidus* has its flowering peak middle of March ($n=257$) while *C. inflatus* is starting to be flowering not before mid-April and reaches its statistical maximum flowering middle of June ($n=255$, statistical mean values for Portugal). In the study area, the probability of hybridization between those two species is higher than in the rest of the country, because the flowering time of *C. inflatus* is starting much earlier than in the North, beginning of March with its peak end of April.

Similar is the situation of flowering times regarding *C. crispus* and *C. inflatus* (www.flora-on.pt, accessed on April 22, 2022). While *C. inflatus* is one of the first flowering in March, much earlier than the populations in North Portugal, *C. crispus* has its maximum flower development from the second half of April onwards until the end of May.

The richness in hybrids of *Cistus* in Southwest Iberia may be due to the overlap of flowering and pollination periods, driven by bioclimatic factors, especially in this Mediterranean-Atlantic ecotone (Vila-Viçosa & Arsénio, 2021), supported by a geologic mosaic of some marine calcareous deposits from the Tertiary on Carboniferous bedrock. But as well the climatic factor has its importance for the high number of species and hybrids due to the strong influence of the Atlantic onto the Mediterranean *Cistus* garrigue with associations

Table 5. Flowering pattern of *Cistus* taxa in 2022 registered near Aljezur, Southwest Portugal.

| Flowering period 2022 | March | | | | | April | | | | May | | | | | June | | | |
|---|-------|-----|-----|-----|-----|-------|-----|-----|-----|-----|-----|-----|-----|-----|------|-----|-----|-----|
| Calendar week | 9. | 10. | 11. | 12. | 13. | 14. | 15. | 16. | 17. | 18. | 19. | 20. | 21. | 22. | 23. | 24. | 25. | 26. |
| Cistus species | | | | | | | | | | | | | | | | | | |
| <i>C. albidus</i> | | | | | | | | | | | | | | | | | | |
| <i>C. crispus</i> | | | | | | | | | | | | | | | | | | |
| <i>C. inflatus</i> | | | | | | | | | | | | | | | | | | |
| <i>C. ladanifer</i> | | | | | | | | | | | | | | | | | | |
| <i>C. monxeliensis</i> | | | | | | | | | | | | | | | | | | |
| <i>C. populifolius</i> sx. <i>major</i> | | | | | | | | | | | | | | | | | | |
| <i>C. salviifolius</i> | | | | | | | | | | | | | | | | | | |
| Cistus Hybrids | | | | | | | | | | | | | | | | | | |
| <i>Cistus</i> x <i>aguilari</i> | | | | | | | | | | | | | | | | | | |
| <i>Cistus</i> x <i>aljezurensis</i> | | | | | | | | | | | | | | | | | | |
| <i>Cistus</i> x <i>dansereau</i> | | | | | | | | | | | | | | | | | | |
| <i>Cistus</i> x <i>daveauanus</i> | | | | | | | | | | | | | | | | | | |
| <i>Cistus</i> x <i>fernandesae</i> | | | | | | | | | | | | | | | | | | |
| <i>Cistus</i> x <i>incanus</i> | | | | | | | | | | | | | | | | | | |
| <i>Cistus</i> x <i>hybridus</i> | | | | | | | | | | | | | | | | | | |
| <i>Cistus</i> x <i>stenophyllus</i> | | | | | | | | | | | | | | | | | | |
| <i>Cistus</i> x <i>laxus</i> | | | | | | | | | | | | | | | | | | |
| <i>Cistus</i> x <i>obtusifolius</i> | | | | | | | | | | | | | | | | | | |
| <i>Cistus</i> x <i>platysepalus</i> | | | | | | | | | | | | | | | | | | |
| <i>Cistus</i> x <i>verguinii</i> | | | | | | | | | | | | | | | | | | |
| some flowers | | | | | | | | | | | | | | | | | | |
| some plants flowering | | | | | | | | | | | | | | | | | | |
| nearly all plants flowering | | | | | | | | | | | | | | | | | | |



Figure 28. Regular cuttings are the biggest threat to these hybrids locally. In 2022, one of two specimens of *C. x daveauanus* was cut back by cleaning activities under an electricity landline.

of the *Ulici argentei-Cistion ladaniferi* occurring in mosaic pattern with associations of the *Ericenion umbellatae* (Costa *et al.*, 2012).

In this upper thermomediterranean Thermotype and lower subhumid Ombrotype conditions (Monteiro-Henriques *et al.*, 2016) the most southern population of *C. inflatus* in the southwest of Portugal has a much earlier flowering season in April than the average flowering season of this species which is in June (FLORA-ON.PT, based on 277 registered flowering exemplars, 26.2.2023). This creates a unique situation in the southwest of Portugal where this species gets in contact with other species of *Cistus* flowering in the same period of springtime (see Table 4).

In a lot of features the new taxon *C. × aljezurensis* shows intermediate characters of its parental. Seen from distance it resembles a smaller *Cistus albidus*, which is absent in this habitat. The main features to distinguish *C. aljezurensis* from the parent species *C. albidus* is the inflorescence being composed by 3 or more flowers on the top and two laterals, with larger peduncles (contracted inflorescence at *Cistus crispus* and pauciflorous or multiflorous, cymoid, sometimes partially subscorpioid in *Cistus inflatus*) and the petals which are a bit bigger than the ones of its parental. The strong pink presence of the flowers makes it easy to find the individuals in the habitat. *Cistus × aljezurensis* flowers about 2–4 weeks earlier than most of *C. crispus* in the area and keeps flowering some weeks longer, as other *Cistus* hybrids (Schwarzer & Schwarzer, own data). Further investigation must be carried out to understand if seeds of this hybrid are fertile, as it is considered a common phenomenon (e.g. Navarro-Cano *et al.*, 2017).

Disturbances are the second driving force that fulfills Anderson's (1949) description of introgressive plant populations. When examining perturbation factors for the specimen of both hybrids presented in this study (*C. × aljezurensis* and *C. × daveauanus*), we could confirm that it is regular cutting. The first hybrid grows along a roadside where the municipality passes regularly with a mowing machine in spring. The cutting is so intense that one hybrid specimen died completely, while two others struggled a long time to bring new shoots from the only woody remains. The second hybrid is under an electricity landline, where regular cutting also takes place to prevent wildfires (Figure 28).

Conclusions

Portuguese botanical research has a long-standing tradition of documenting hybrids within the genus *Cistus* (e.g., the works of Dansereau, Daveau, Pereira Coutinho, Pinto da Silva). The present study contributes to this tradition. This study updates the classification of six *Cistus* species and seventeen nothotaxa in Southern Portugal, representing a relatively high number compared to other regions of the Iberian Peninsula.

A combination of environmental factors serves as ecological drivers for this hybrid richness: the strong Atlantic influence on the Mediterranean climate, the proliferation of *Cistus* scrubland following the abandonment of agricultural lands, the intensification of cuttings as a wildfire prevention measure, and the

high species diversity with overlapping flowering periods. The occurrence of natural nothotaxa within the genus *Cistus* exemplifies hybridization as an evolutionary driver. Similar observations have been made for other plant genera in the same region (e.g., *Lavandula*, personal observation, or *Quercus*; Vila-Viçosa *et al.*, 2023).

Authorship

US, CS: Conceptualization, methodology, fieldwork, formal analysis and investigation, writing, review and editing.

Conflict of interest

None.

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