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Silene velutina Pourret ex Loiseleur (Caryophyllaceae) — example of a Messinian destiny

Helen Kiefer & Gilbert Bocquet

RÉSUMÉ

KIEFER, H. & G. BOCQUET (1979). *Silene velutina* Pourret ex Loiseleur (Caryophyllaceae) — exemple de destinée messinienne. *Candollea* 34: 459-472. En anglais, résumé français.

L'origine et l'histoire du chasmophyte endémique corse *Silene velutina* Pourret ex Loiseleur sont discutées sur la base du modèle messinien et sa répartition actuelle mise en rapport avec son histoire. La synonymie est fournie. Un choix de schémas de migration pendant la crise de salinité messinienne est présenté pour différentes plantes.

ABSTRACT

KIEFER, H. & G. BOCQUET (1979). *Silene velutina* Pourret ex Loiseleur (Caryophyllaceae) — example of a Messinian destiny. *Candollea* 34: 459-472. In English, French abstract.

The origin and history of the chasmophytic Corsican endemic *Silene velutina* Pourret ex Loiseleur are discussed on the basis of the Messinian Model, and its present distribution is related to this history. The synonymy is given. A number of models for the migration of different plants during the Messinian salinity crisis are presented.

The name *Silene velutina* Pourret ex Loiseleur has often been misapplied in the past. The true *S. velutina*, a chasmophytic species endemic to Corsica, has now disappeared from the calcareous cliffs at Bonifacio, locus classicus

and only site known for this plant according to herbarium records. On the other hand, a population of this species has recently been found on the "îlot du Toro", a tiny island off Corsica.

Relationships of the species

In its ecology and morphology *S. velutina* shows close affinities to a whole range of highly endemic chasmophytic species of the western Mediterranean area: *S. fruticosa* L., *S. mollissima* (L.) Pers., *S. hifacensis* Rouy ex Willk., *S. pseudovelutina* Rothm., *S. gibraltarica* Boiss., *S. auriculata* Sibth. & Sm., *S. sessionis* Batt., *S. aristidis* Pomel and *S. salzmännii* auct. non Otth in DC.

This whole group of extremely specialized relicts, in its turn, is related to the steppic circum-Mediterranean *S. italica/patula*-complex, from which it probably originated. All these species must therefore be regarded as the descendants of a very old syngameon.

History

The history of this syngameon is a prime example of Messinian migration and speciation. The ancestors of the *italica/patula*-complex probably belonged to the colline steppes of the east. Their migration westwards and into North-Africa became feasible through the formation of the Alps and the expansion of steppes during the Messinian.

It has to be stressed that the model for the migration of orophytic plants given in BOCQUET & al. (1978) is but an example of possible paths, which applies e.g. to the genus *Digitalis* L. For each taxon, the various factors such as geographic origin, ecology and altitudinal zone have to be considered. It is in fact this possibility of multiple application that is the prime value and attraction of the Messinian Model (BOCQUET & al., 1978).

Thus, plants of the colline and mountain zone, often bound to habitats subject to erosion, generally follow the pattern given in Figure 1a. *Silene velutinoides* Pomel (CORRIAS & CORRIAS, 1977), *Sedum multiceps* Cosson & Durieu, as well as the Sardo-Corsican *Morisia monanthos* (Viv.) Ascherson together with the closely related North-African *Cossonia* Durieu (cf. WIDLER & BOCQUET, 1979a) are examples for the eastern part of this connection, whilst *Abies pinsapo* Boiss. is a representative of the South-Iberian/North-African distribution. *Helleborus lividus* Aiton and *H. corsicus* Willd., on the other hand, are typical for the often encountered Balearic-Corsican relationship.

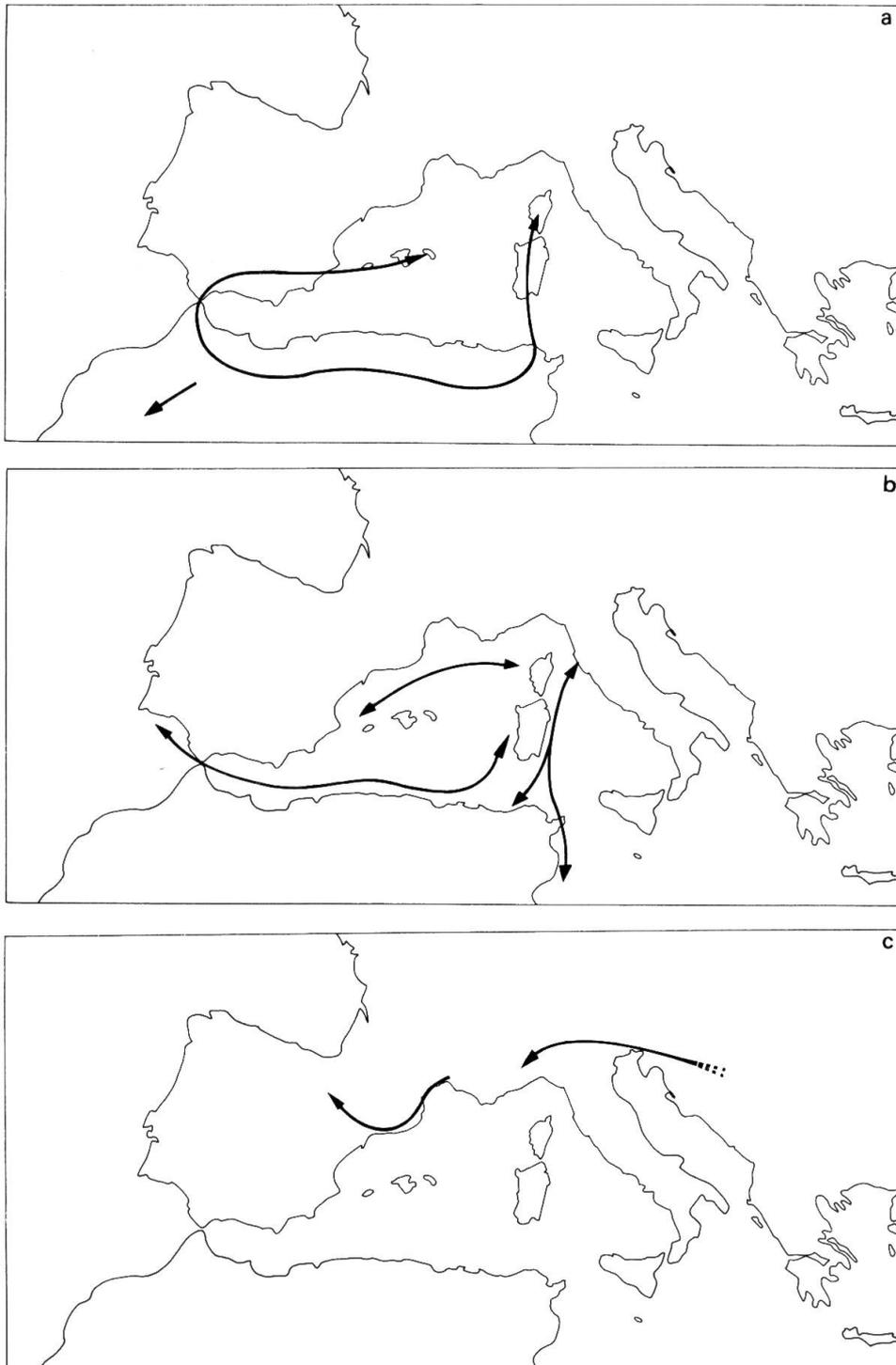


Fig. 1. — Models for possible paths of Messinian migration for different plants.

The same model could also apply to *Arenaria balearica* L., though the connection could be north-Mediterranean in this particular case. The above relationships and distribution-patterns cannot be explained with a direct connection for plants of these altitudinal zones and ecological demands. The possibility of long-distance dispersal, though not categorically rejected for isolated cases, has been extensively discussed and dismissed as a prime contributor to the Corsican flora by BOCQUET & al. (1978).

A direct connection between the Betic and Tyrrhenian regions would have been feasible, though, for plants of sandy habitats such as *Armeria pungens* (Link) Hoffmanns. & Link and *A. fasciculata* (Vent.) Willd. (Fig. 1b). The north-south path for sand-plants is reflected in the distribution patterns of e.g. *Pycnocomon rutifolium* (Vahl) Hoffmanns. & Link, *Echinophora spinosa* L. and *Silene corsica* DC./*S. succulenta* Forskål, whilst *Cynomorium coccineum* L., according to EBERLE (1965), would have expanded along both axes.

Silene nemoralis Waldst. & Kit. (= *S. crassicaulis* Willk. & Costa) is a typical example for steppic and rock-plants that migrated along the southern Alps at the foot of the hills, in connection with them but not actually on them (Fig. 1c). Though some taxa did not come all the way, the particularity which this type of plant is the strict and conspicuous limit to their furthest westward expansion: the region of Jaca in the Pyrenees, where the Atlantic domain begins. Their distribution is possibly linked to Messinian canyons (BOCQUET & al., 1978).

Of course, all these models are limited to "active" taxa migrating in this particular era. They do not contradict any models of post-Messinian migration as e.g. RIVAS-MARTINEZ (1973) for orophytic taxa in Spain, which would probably apply to e.g. the *Salvia lavandulifolia* Vahl-group (Lippert, personal communication).

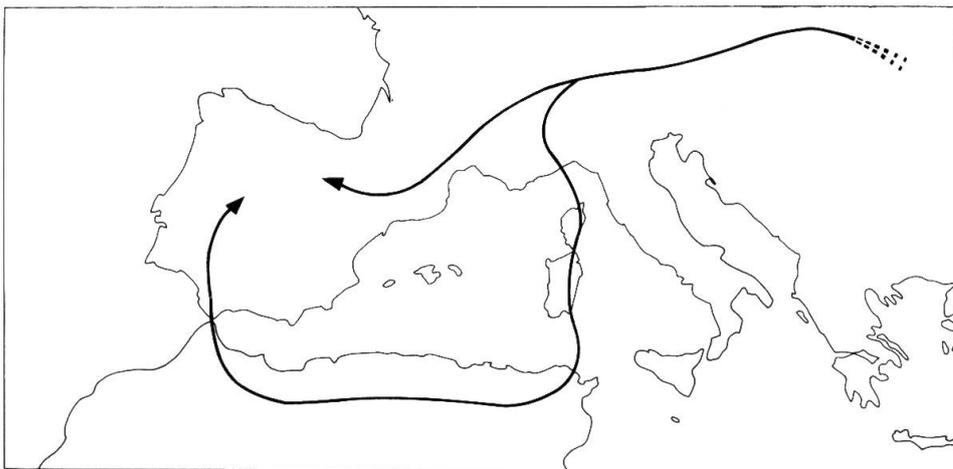


Fig. 2. — Model for the origin and expansion of the *Silene italica/patula*-complex.

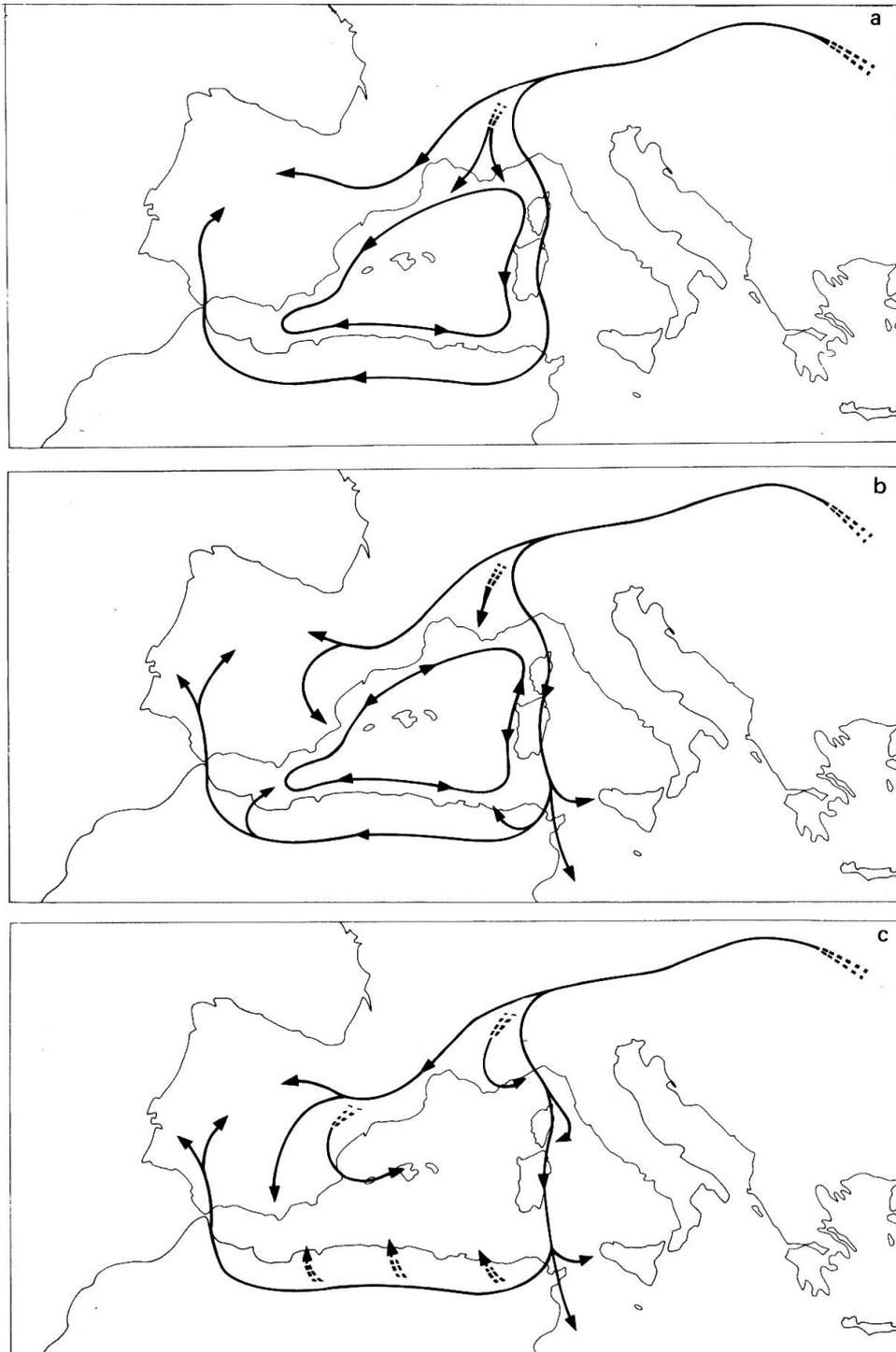


Fig. 3. — The three possible models for the branching-off of the chasmophytic species from the *Silene italica/patula*-complex.

For the *Silene italica/patula*-complex, a model is given in Figure 2. The arrows follow the probable position of colline steppes in the early Messinian, the reason for the difference to model 1c being mainly the altitudinal zone. The two taxa met in Spain, *S. italica* (L.) Pers. being north- and *S. patula* Desf. south-Mediterranean respectively. The exact border-line will have to be determined in the detailed study of this group, which has now been initiated. Thus, the meeting-point of the arrows may have to be adapted, though new data is most unlikely to change the actual position of the paths.

The catastrophic environmental events of the salinity crisis were particularly suited to trigger off an evolutionary thrust in young and active taxa. Furthermore, the exposed slopes of the desiccated Mediterranean basins offered new ground for colonization (BOCQUET & al., 1978). Conditions were thus ideal for the differentiation and expansion of new chasmophytic ecotypes. This is most likely how the chasmophytic species in this group of *Silene* L. originated. There are three possible models (Fig. 3): *a*) a single event of branching off from the *italica/patula*-complex with subsequent expansion and speciation; *b*) each of the endemic species branching off separately and *c*) a combination of the two, suggesting a polyphyletic origin for the chasmophytes but, at the same time, a phase of expansion and contact for the different branches. Model *c* is certainly the most likely one, particularly since the cyclic changes in the environment, during the Messinian, must have caused considerable movement in the flora, merging and separating the populations repeatedly.

It is noteworthy that, though the situation in *Brassica* L. (cf. WIDLER & BOCQUET, 1979b) is similar as far as the circum-Mediterranean group of chasmophytic endemics is concerned, the models differ slightly. This is partly due to the fact that the ecological demands of the two groups are not quite equal, partly to the difference in the situation at their origin: whilst the section *Lignosae* Widler & Bocquet of *Brassica* started off from the relatively limited area of *B. oleracea* subsp. *robertiana* (Gay) Rouy & Fouc. (WIDLER & BOCQUET, 1979b), the chasmophytic endemics of *Silene* arose from a circum-Mediterranean syngameon.

The environmental stress of the last phases of the salinity crisis and particularly the sudden marine transgression at the beginning of the Pliocene (HSÜ & al., 1977) reduced the suitable habitats for these specialized taxa drastically and the populations became thus isolated in typical relictual sites.

The decline

Silene velutina is well documented from its only site¹ and locus classicus, the calcareous cliffs of Bonifacio (Corsica), by herbarium records from 1813 up to 1918. Two localities, "St. Roch" and the "Sémaphore" are repeatedly mentioned. Since local seed-distribution is very effective in this species, it is to be expected that most of the adequate niches on these 2 km of favourably exposed, but not easily accessible cliffs were occupied by this plant.

However, extensive searches for *S. velutina* in the years 1973-1977 along the coast from Figari to Capo Blanco (Fig. 4), with the exception of only a few private and inaccessible places, remained unsuccessful. Already in the early 1950's Contandriopoulos failed to find the species despite special efforts, and neither Marcelle Conrad nor Roger de Vilmorin, both very knowledgeable on the Corsican flora, have ever seen it there (all personal communications). We must therefore assume that *S. velutina* disappeared from the Corsican mainland at some time between 1918 and 1950. But what were the reasons for this extinction?

There have been no drastic changes in the environment since the beginning of the century. As far as we can tell, the climate has not changed. A certain amount of tourism has developed in Bonifacio, but this is hardly likely to have such an impact on a species growing in nearly inaccessible places. The town of Bonifacio itself has not actually expanded yet. The plateau above the cliffs is less intensely cultivated than it used to be, which, however, could only affect *S. velutina* positively, if at all. The decrease in grazing animals, particularly goats, needs not be considered important since the plants grew mostly out of reach of these animals anyway. Thus, none of this could account for the extinction of a population spread along 2 km of coastline.

As for the possibility of some catastrophe in the cliffs: the latter are indeed subject to considerable erosion, and on rare occasions some part or other of the cliff actually collapses. Even though this may be quite spectacular, it is always confined in its range, the 2 km of cliffs never being affected as a whole. The process of erosion is in fact a very slow one: some measure of the time-scale involved is given by the fortifications on the cliff, whose exposed stairways, look-outs and pinnacles, dating back to the last century, are still partly intact. As a matter of fact, this particular type of erosion ought to create rather favourable conditions for a chasmophytic species like *S. velutina* by continuously creating new sites for colonization.

¹We have seen a specimen each from Porto-Vecchio and Vizzavona. Though the two plants are *S. velutina*, we consider their localities as erratic or possibly erroneous and hence unimportant. According to Arrigoni (personal communication, 1978), there could possibly be another locality of *S. velutina* on one of the islands north of Sardinia, though no proof exists.

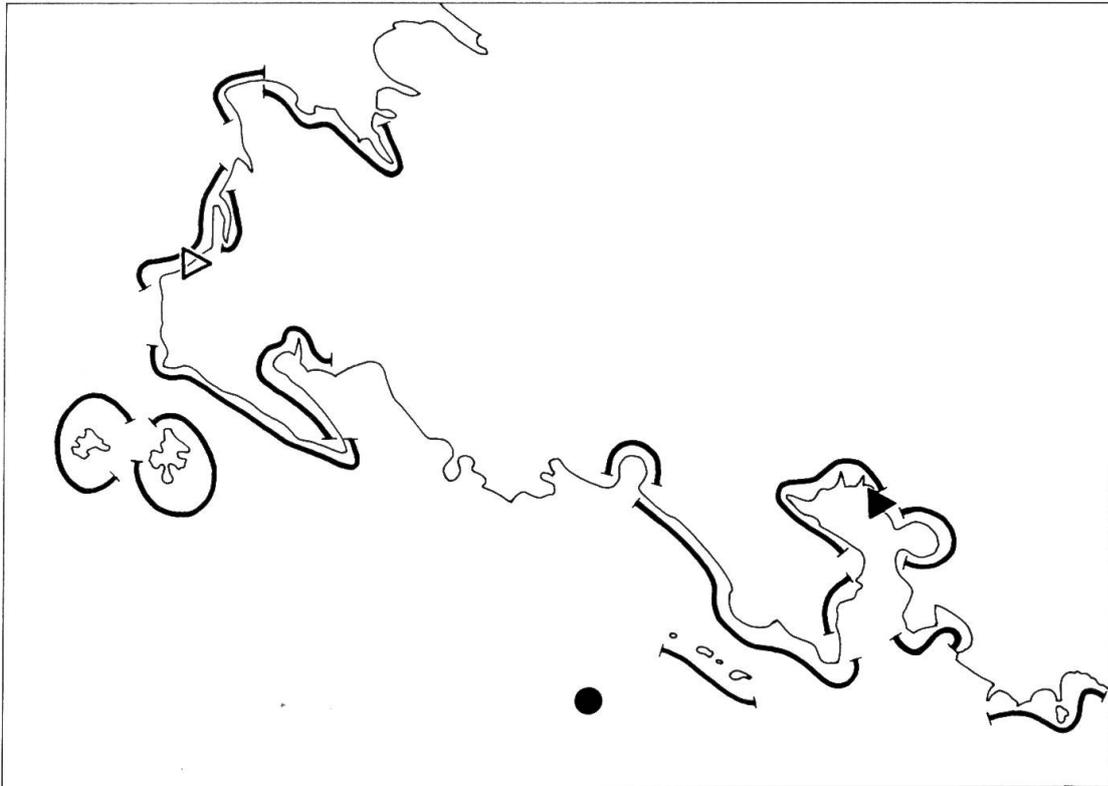


Fig. 4. — The localities of *Silene velutina* in south-eastern Corsica.
 △ Bonifacio: locus classicus, now extinct. ● ilot du Toro: only present-day population. ▲ Porto-Vecchio: herbarium record from 1903, two planted specimens today. —→ Stretches of coast-line searched for *Silene velutina*.

Sometimes the loss of a rare species is blamed on the overenthusiasm of botanical collectors. We are, however, not aware of any case where this accusation has been substantiated with facts and proofs. As for *S. velutina*: even if the 65 collections cited here were not all the material ever collected, considering the time-span involved, we would have to acquit the botanists in this case. Furthermore, by the nature of *S. velutina* it is extremely unlikely that any roots were ever collected, and most of the plants would have been safeguarded by their inaccessibility anyway.

There is, of course, the possibility of some slight but crucial change in conditions which we have not recognized. On the whole, however, it is much more plausible that the reason for extinction lies in the plant itself and in its history.

The endemic species in this group of *Silene* differentiated from their steppic ancestors in the course of the Messinian salinity crisis, by specializing as chasmophytes and conquering the new ground provided by the desiccated Mediterranean. At the time of the division into sub-units, which repeatedly expanded, merged and retreated in response to the cyclic environmental changes, evolution in the syngameon was probably rapid. Various selective

pressures would come to act and genetic drift would have become a contributing factor. A certain amount of migration between the populations ensured the possibility of new gene-combinations and may have prevented such deleterious effects of genetic drift as the random loss of advantageous alleles (WRIGHT, 1931; SHEPPARD, 1975).

The extreme conditions towards the end of the salinity crisis must have forced the chasmophytic plants to retreat. A complete separation of the sub-units, however, would, conditions being similar, have led to slower parallel evolution (WRIGHT, 1931).

With the Pliocene inundation of the Mediterranean, these populations found themselves in such refuges as remained above the new sea-level, i.e. on short stretches of costal limestone-cliffs and in ravines, many of which had been carved into the continental plate during the Messinian (CLAUZON, 1978). *Silene velutina* is certainly such a relict species, confined for the last 4-5 Mio. years to a comparatively short stretch of coastline on the island of Corsica, with absolutely no possibility of gene-exchange with related species. In small isolated populations, however, genetic drift, the random process of fixing and eliminating genes, begins to play a major role. The population has a strong tendency towards homozygosity and thus to become a stable non-evolving complex, lacking genetic variability. Since mutations, also deleterious ones, become rapidly fixed as well, these non-adaptive processes are most likely to lead the population concerned into extinction (WRIGHT, 1931; GRANT, 1977a + b). Thus, the disappearance of *S. velutina* from Bonifacio becomes explicable, if not indeed inevitable.

The phenomenon of reproductive drift, i.e. random deviations from reproductive frequencies, can, similar to genetic drift, involve a great risk of elimination for small populations (RUNEMARK, 1969, 1970). In a perennial species like *S. velutina*, though, this factor could probably only be decisive if the population had already been drastically reduced, for example by an illness.

The population on the "îlot du Toro"

In 1969, ZEVACO first reported *Silene velutina* from the "îlot du Toro", a group of granitic rocks, 7 km off the coast between Porto-Vecchio and Bonifacio, in all not more than 400 m in diameter and with a maximum elevation of 40 m. The population consists of about 1000 plants.

For several reasons, we consider this population to be a fairly recent one, and not part of an original wider distribution of *S. velutina*.

The high sea-levels of the quaternary interglacial periods, with a maximum of 20-30 m above the present sea-level during the Riss/Würm interglacial (GUILCHER, 1968), would have left but the tapering peak of the main rock exposed. Since *S. velutina* does not grow in the immediate spray-zone but only in more sheltered localities at least 15 m above sea-level, any existing population would inevitably have been destroyed at that time.

Though Toro was connected with the Corsican mainland during the Würm glacial when the sea-level dropped to approximately -100 m (LANZA, 1972; GUILCHER, 1968), *S. velutina* would have had to expand over wide stretches of unsuitably exposed granitic territories to reach the island. This is certainly most unlikely for a relict species adapted to calcareous cliffs, which already then must have had lost a good deal of its genetic vigour through its long isolation. The fact that *S. velutina* manages to survive on the granitic Toro-island, at the moment, can be ascribed to the striking lack of competition. The flora of Toro is extremely poor with, in all, a mere 13 species being represented (LANZA, 1972). This is and was certainly not the case for the coastal area of the Corsican mainland, and indeed the plant has never been found on the granitic rocks extending on both sides of the calcareous cliffs at Bonifacio. Thus we think that the population on Toro was established after the separation of the island from Corsica became permanent.

With no land-connections, however, the species would have had to arrive on Toro by means of long-distance dispersal. Since the seeds of *Silene* do not float, transport by water is not possible (a remarkable exception is *S. holzmannii*, whose capsules do not open and can be carried as a whole by the sea; cf. GREUTER, 1972). Wind-distribution over long distances is very doubtful too: the seeds are certainly not adapted to this mode of transport, being heavy and without any specialized structures. According to LEVIN & KERSTER (1974), the range of wind-dispersal has anyway been considerably overrated in the past, and it is thus most unlikely that the seeds of *S. velutina* were carried well over 20 km, a distance regarded by RUNEMARK (1970) as an "effective barrier to migration even for species with easily dispersed seeds". On the other hand, birds do not eat the seeds of *S. velutina*, though we cannot definitely exclude transport in the plumage of a bird. Apart from the fact that the efficiency of long-distance dispersal in general has been doubted of late (RUNEMARK, 1969), it would be difficult to explain why *S. velutina* was only carried to Toro by wind, water or birds, and not to e.g. the Cerbicale islands offering similar conditions.

The only discerning vector in "long-distance dispersal" is man. We think indeed that it was man who brought *S. velutina* to Toro, and there is one particular man who offers himself to speculation: Stephani, the famous Corsican collector of the early 1900's. He repeatedly collected *S. velutina* from the cliffs at Bonifacio, he cultivated plants for distribution, and it is certain that he visited some islands of South-Corsica quite frequently. He could very well, inadvertently or on purpose, have brought *S. velutina* to Toro, though this, of course, must remain speculation.

As for the future of this population: it looks rather bleak. With tourism reaching the remotest corners of Corsica, it is probably only the question if man will forestall the natural decline of this small isolated population. One danger was recently averted, when Mrs. Conrad prevented Toro from becoming a target for the guns of the French Navy, by intervening right at the very top with the Admiral.

Appendix: pars systematica

- Silene velutina** Pourret ex Loiseleur-Deslongchamps, J. Bot. (Desvaux) 2: 324. 1809; Flor. gallica ed. 2, 1: 313. 1828. Holotypus: “Silene vivace / Dans les roches / Bonifacio”, “Silene velutina Pourr. / no. 26”, s.d. Lasalle s.no., FI-Webb 019533 [ex hb. Desfontaines]; iso.: “Silene velutina Pourret. / sic in hb. D. Desfont.” [ex hb. Vaillant], P.
- = *Silene salzmannii* Otth in DC., Prodr. 1: 318. 1824; Badaro in Moretti, Giorn. Fis. 9: 78. 1826. Holotypus: “Silene fruticosa L. / in rupibus circa Bonifacio / Mr. Saltzmann [Salzmann]. 1821”, G-DC; iso.: G [ex hb. Haller fil.] = *S. italica* subsp. *salzmannii* Archangeli, Compendio ed. 1: 93. 1882, ed. 2: 313. 1894.
- *Silene mollissima* auct. non (L.) Pers., quod est planta balearica.
- *Silene italica* Viviani, Fl. Corsicae: 6. 1824, non L.
- non *Silene salzmannii* “Badaro” [sphalm.] apud auct. imprimis Florae Europaeae, quod est *Silene tyrrhenia* Bocquet & Kiefer (parturiunt auctores!).

SPECIMINA VISA

Bonifacio: “rariss. / Bonifacio”, 1813, *Bernard C8* (G); “Bonifacio”, 1846, *Bernard 97* (G); “Bonifacio”, 1843, *Bernard 176* (MPU); “Bonifacio”, 1845, *Bernard* s.no. (P); “Corse”, 1833, *Bonpland* s.no. (P); “Silene Salzmannii Otth.”, s.d., coll. ign. s.no. (LY, hb. Gandoger); “M’a été envoyé de Bonifacio”, s.d., coll. ign. s.no. (G); “in rupibus / Bonifacio”, s.d., coll. ign. s.no. (G); “Silene amoena L.”, ex hb. Pourret, s.l., s.d., coll. ign. s.no. (P); “Bonifacio”, s.d., coll. obsc. s.no. (G); “Corse”, 1837, *Forestier de* s.no. (G); “Corsica / culta”, s.d., *Godat* s.no. (MARS); “Corse, Bonifacio”, 1843, *Jordan* s.no. (G); “de Corse / cult. ex sem.”, s.d., *Jordan* s.no. (P); “Rochers maritimes, Bonifacio”, 06.1849, *Kralik 494* (G, MARS, P); “In rupestribus maritimis, Bonifacio”, s.d. *Kralik* s.no. (ZT); “Silene vivace / Dans les rochers / Bonifacio”, “Silene velutina Pourr. / no. 26”, s.d. *Lasalle* s.no. (FI-Webb 019533 ex hb. Desfontaines, holotypus *S. velutinae*); “Silene velutina Pourret. / sic in hb. D. Desfont.”, s.d., [*Lasalle*] s.no. (P, isotypus *S. velutinae*); “Bonifacio”, 05.1847, *Requien* s.no. (G); “Bonifacio”, 06.1849, *Requien* s.no. (G); “Bonifacio”, s.d., *Requien* s.no. (G, MARS); “Bonifacio — Rochers maritimes”, 18.06.1866, *Revelièrre* s.no. (LY); “Bonifacio”, “Les roches maritimes. rare”, 09.07.1880, *Reverchon 260* (G); “Bonifacio, rochers maritimes”, 26.07.1880, *Reverchon 260* (G, LY, P); “Bonifacio, sur les rochers / maritimes, sur le calcaire. Juin. / Rare”, 06.1894, *Reverchon 260* (P); “In saxosis maritimis prope “Bonifacio”, “Locus classicus Silenis velutinae Pourr!”, 06.1894, *Reverchon 3207* (G, MPU, P, Z, ZT); “St Roch près Bonifacio”, 21.06.1894, *Saint-Lager* s.no. (G); “Silene fruticosa L. / in rupibus

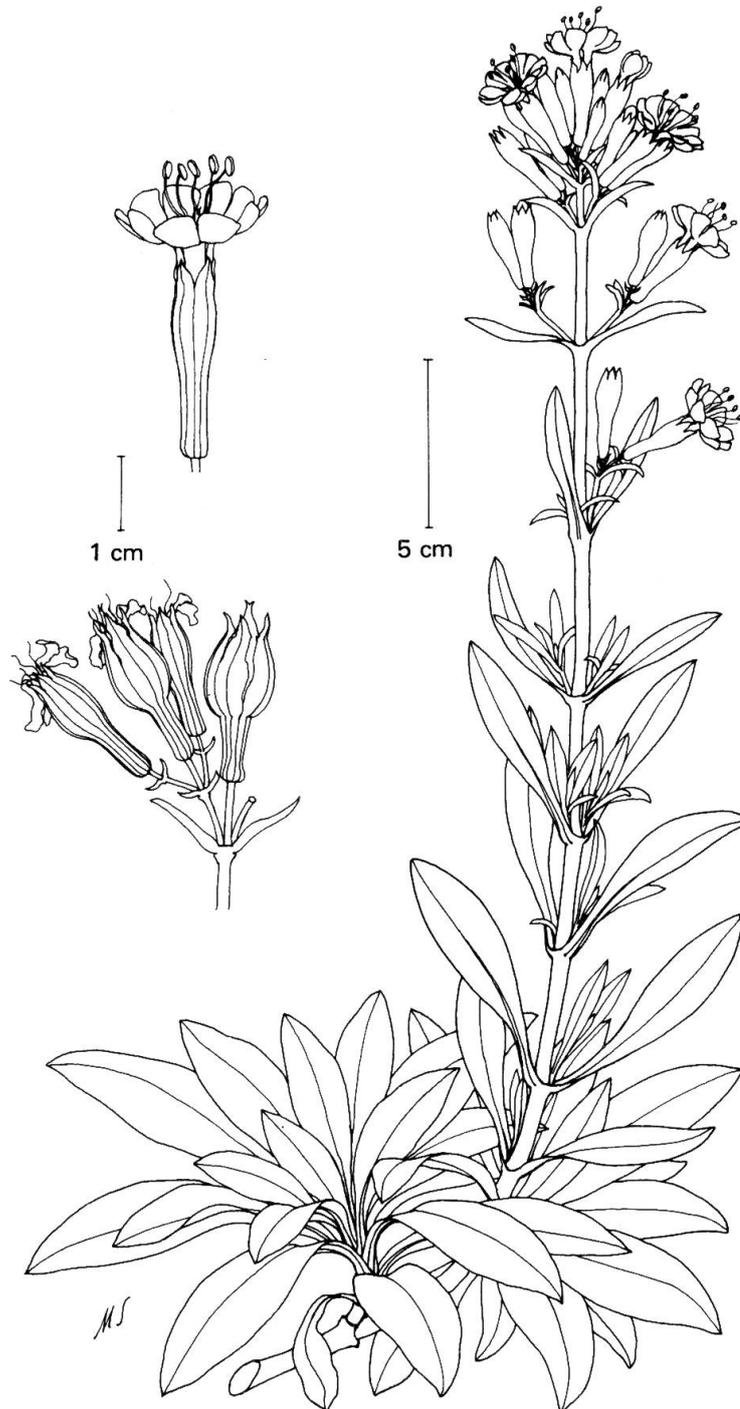


Fig. 5. — *Silene velutina*, îlot du Toro.

circa Bonifacio" 1821, *Salzmann* s.no. (G-DC); "Silene fruticosa / Bonifacio in rupibus", s.d., *Salzmann* s.no. (G); "Bonifacio", s.d., *Salzmann* s.no. (E, MPU); "Sur un Rocher de St / Roch de Bonifacio", 1901, *Stefani* 183 (LY); "sur un / Rochez Calquaire pres de St Roche", 1902, *Stefani* 183 (P); "Rocher calcaire de St. Roch", 19.06.1911, *Stefani* 560 (P); "Rochers St. Roch", 24.06.1911, *Stefani* 560 (P); "Rochers maritimes à St. Roch", 17.06.1901, *Stefani* s.no. (MPU); "Rochers Calcaires de St. Roch", 14.06.1902, *Stefani* s.no. (G); "Rochers de St-Roch, près Bonifacio", 15.06.1903, *Stefani* s.no. (G, Z, ZT); "les Rochers calquaires / de Bonifacio", 10.06.1911, *Stefani* s.no. (Z); "Bonifacio / Route du Sémaphore", 1918, *Stefani* s.no. (G, MPU); "Sillénne Velutina, / non de le Pourr. ouvrages de Marsilly / Recolte le 15 Juin / sur les Rochez de St. / Roch de Bonifacio", s.d., *Stefani* s.no. (LY); "Bonifacio", s.d., *Thouars* s.no. (P).

Toro: "Corse, îlot du Toro: abondant dans les rocailles / granitiques de tout l'îlot comme chasmophyte; peu de terre, / mais nitrophile (perchoir à oiseau), végétation / limitée à quelques espèces de rocailles côtières.", 10.07.1974, *Bocquet* 16399, 16400, 16401, 16402, 16403 (incl. specim. *Turicula*), 16404, 16405, 16406, 16407 (ZT); "Corse, îlot du Toro au sud des Cerbicales: chasmophyte dans les vires et les fissures des rochers granitiques. Abondant", 18.07.1975, *Bocquet* 18050, 18051, 18052, 18053, 18054, 18055, 18056 (ZT); "Corse, îlot du Toro", rochers granitiques, 18.07.1975, *Bocquet* (BM, FI, K, MPU, P, SEV, ZT); "îlot du Toro, au large de / Porto-Vecchio — Corse", 24.05.1969, *Conrad* s.no. (MPU).

Porto-Vecchio: "Corse, pointe ouest de la baie de Stagnolo, / golfe de Porto-Vecchio; / 3 pieds, dont deux symétriquement plantés / de chaque côté d'un portail donnant sur la / plage. Pas de jeunes plantes, donne l'impression d'être planté! / Fleur rosée. / (Les propriétaires de Villas vont volontiers / pêcher à l'îlot du Toro.)", 30.05.1977, *Bocquet* 19667 (ZT); *ibid.*, 27.05.1977, *Bocquet* 20125 (ZT); "environs de Porto-Vecchio Corse", 07.06.1903, *Jaccard* s.no. (ZT).

Vizzavona: "Vizzavona", 14.06.1917, *Forsyth-Mayor* 8/287 (K).

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