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## Reproductive biology of *Petrocoptis crassifolia* Rouy (Caryophyllaceae), a chasmophilous endemic plant of the Central Pyrenees

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### Abstract

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The reproductive biology of *Petrocoptis crassifolia* Rouy (Caryophyllaceae), an endemic plant of the Central Pyrenees (Spain), was studied. Its nectariferous flowers show an ultraviolet pattern in the corolla and an incipient zygomorphism in the arrangement of petals and stamens. *P. crassifolia* may produce seeds by autogamy but in smaller numbers than when it is pollinated by insects (mainly Hymenoptera). The fruit-set ranges between 43–80%, depending on the years and populations studied. Fruits develop towards the rock face, and seeds exhibit myxospermy; both these traits are adaptations that facilitate the deposition of seeds in rocky substrata. Survival of the seedlings in rocky fissures at the end of the first year is 10%. Reproductive traits suggest that this species is well adapted to its habitat, and that it is not endangered. Its rarity seems to be associated mainly with a lack of dispersal mechanisms for colonizing suitable but remote habitats.

*Key words:* Reproductive biology, *Petrocoptis crassifolia*, endemic plant, Pyrenees.

### Introduction

The Pyrenees, like other mountains in the Iberian Peninsula, are one of the areas with the largest diversity of vegetation and endemism in Europe (Favarger 1972, Gómez-Campo and Malato-Beliz 1985, Villar and García 1989). Until now, studies of endemic plants in the Pyrenees have focused on taxonomy and biogeography (see, for example, Montserrat and Villar 1972, Küpfer 1974, Delay and Vivant 1978, Vivant and Delay 1980, Baudière and Cauwet-Marc 1987, Villar 1988), and only recently have they begun to focus on biology and ecology (Dajoz 1991, García and Antor 1992, García et al. 1992), even though this kind of knowledge is very important in deciding their status and their possibilities of survival (Gómez-Campo et al. 1987).

*Petrocoptis crassifolia* Rouy (Caryophyllaceae) is a perennial herb belonging to a genus endemic to the Iberian Peninsula (NE Spain; see Montserrat and Fernández Casas

1989; Saule 1991). It occupies a narrow geographic range (the central Pyrenees) and has a high habitat specificity (crevices of limestone cliffs and overhangs), allowing us to catalogue this species as "rare" (*sensu* Rabinowitz 1981). Since several studies have demonstrated that the rarity of some species is associated with reproductive problems (see, for example, Ross 1936, Davies 1960, Greig-Smith and Sagar 1981, Herrera 1987, 1989), this paper deals with the reproductive biology of this singular endemic plant, and discusses the causes of its rarity.

We have investigated the most important populations of *P. crassifolia*, located throughout the Añisclo Valley (Ordesa-Monte Perdido National Park, Spain) and "Las Devotas" (Lafortunada, Cinca Valley), where we have recorded floral traits, pollinators, dependence on insect visits for reproductive success, fruit set, seed set, and the survival of seedlings.

### Floral traits

The flowers of *P. crassifolia* are composed of a tubular calyx and five free petals each of which bear two coronal scales. Although the corolla has a more or less uniform pinkish-purple colour, UV photographs show "nectar-guides" at the mouth of the floral tube within which nectar is found (Fig. 1). This UV pattern, invisible to the human eye but visible to many insects, is due to the absorption of UV wavelengths by coronal scales,

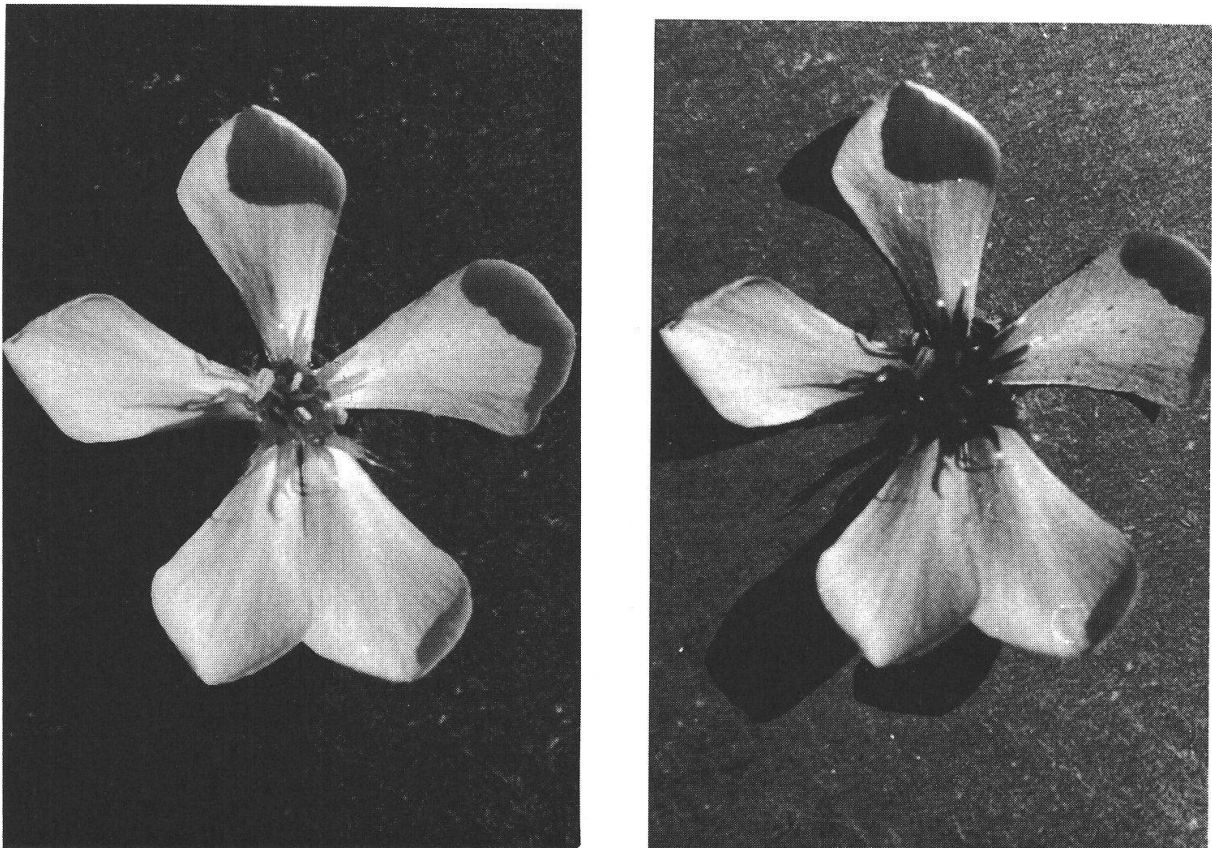


Fig. 1. Visible light (left) and ultraviolet (right) pattern in *P. crassifolia* flower. The right-hand photograph was taken using a filter B+W 403 and a film TMAX 400 ASA (Kodak).

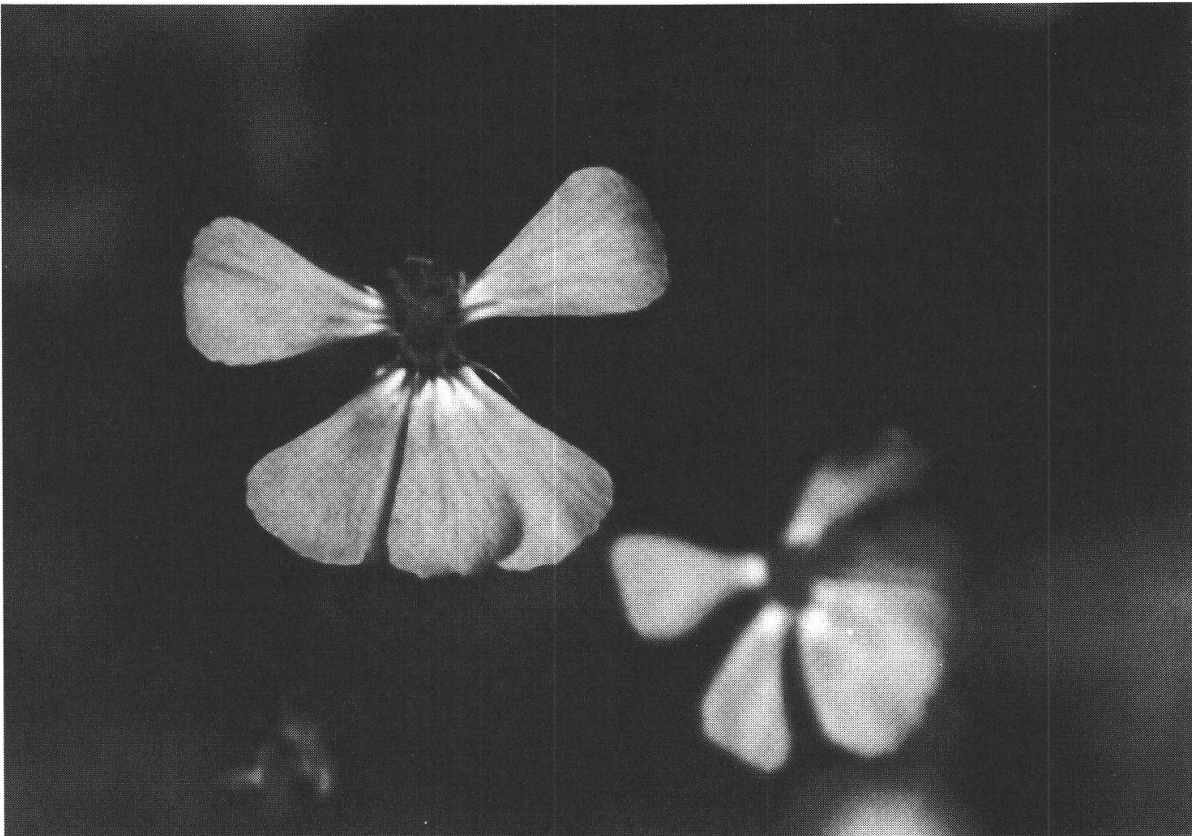


Fig. 2. Example of frequent floral symmetry in *P. crassifolia*: the petals are aggregated in the lower part of the corolla and the anthers in the upper part of the floral tube.

contrasting with the rest of the corolla that reflect them. Detailed UV patterns, composed of reflecting and absorbing regions, can be found in many plant species (Horovitz and Cohen 1972, Jones and Buchmann 1974, Fröhlich 1976, Kay 1984), helping to direct the pollinator's behaviour in a manner that assures pollen transfer (Silberglied 1979).

Because this plant grows on vertical and overhanging walls, its stems are usually pendulous, and the petal plates of the corollas are usually vertically oriented (average  $\pm$  standard deviation:  $90^{\circ}39' \pm 8^{\circ}2'$ ; range:  $80^{\circ} - 109^{\circ}$ ;  $N = 60$ ; calculated following Batschelet 1981). Floral symmetry is not strictly radial, as has usually been assumed, but slightly zygomorphic (Fig. 2). This bilateral symmetry comprises two characteristics: two or three petals are grouped in the lower part of the corolla, and all anthers are located in the upper part of the floral tube. Both stamens and petals are radially arranged at the bottom of the floral tube, but change their orientation within it. This incipient zygomorphy seems to be associated with the vertical position of the petal surfaces and also with the behaviour of the pollinators, because it has been found in other species of the genus that resemble *P. crassifolia* and with similar pollinators (García et al. 1992).

The main reward that flowers of *P. crassifolia* offer to pollinators is nectar, accumulated at the bottom of the floral tube. Nectar measurements were made in cut inflorescences kept in plastic bags for 24 hours at ambient temperature (nectar measured in this way is usually less abundant and more diluted than in the field; see Cruden et al. 1983 for a review of this subject). Each flower produces about two microlitres of nectar per day (average  $\pm$  standard deviation:  $2.3 \pm 1.0 \mu\text{l}$ ;  $N = 36$ ; measured in calibrated micro-

pipets), and the concentration of sugars is about 16% ( $15.7 \pm 2.0\%$ ; measured with a Bellingham and Stanley pocket refractometer).

## Reproduction

The main pollinators of *P. crassifolia* are Hymenoptera (68% of visits to flowers), principally *Anthophora plumipes* and *Bombus pratorum*, followed by Lepidoptera (27%; principally the hawkmoth *Macroglossum stellatarum*) and Diptera (5%; *Bombylius venosus*). These pollinators are very similar to those visiting *P. grandiflora* (Gutián et al. 1992). All of these were recorded as diurnal visitors during 20 censuses of 15' in 1990 and 1991, but we do not know if *P. crassifolia*, like some *Silene* species, is also pollinated by nocturnal insects (see, for example, Pettersson 1991). These insects hang from the coronal scales (as the petal surface is vertical) in order to suck the nectar from the floral tube.

The fruit-set in *P. crassifolia* ranges from 43% to 80% (ratio fruits/flowers), depending on population and year (Table 1). Each fruit usually contains between 5 and 8 seeds, which means that more than half of the ovules develop into seeds (ratio seeds/ovules: 59.2% during 1991 in Añisclo, N=131 fruits examined). Nevertheless, a given population may have a considerable interannual variability in the fruit-set (Las Devotas II:  $\chi^2 = 98.8$ ; d.f. = 1;  $p < 0.001$ ), while no statistical difference was found between populations for the same year (1990:  $\chi^2 = 1.39$ ; d.f. = 1; n.s.).

Some fruits can be formed by self-pollination (22% of the 82 flowers that were enclosed in a fine nylon mesh produced capsules); however, in this way *P. crassifolia* produces significantly fewer fruits than when it is pollinated by insects ( $\chi^2 = 558$ ; d.f. = 1;  $p < 0.001$ ). Although autogamy is possible, 53% of self-pollinated flowers did not produce mature fruits although the ovary began to inflate, which indicates that self-compatibility is not totally functional in *P. crassifolia*. In addition, the seed-set was also lower in enclosed flowers ( $3 \pm 2.4$  seeds per fruit, N=14) than in free flowers (see Table 1).

The dispersal of seeds takes place near the rocky substrate, because capsules develop towards the wall, where they open (Dendaletche 1970). The seeds each have a tuft of hairs that become mucilaginous in contact with water (myxospermy), which allows them to stick to humid surfaces. We have occasionally observed that seeds may be dispersed by ants. On the other hand, anemochory seems unlikely because the seeds lack adaptations for this and are relatively heavy (seed mass: 1.5 mgr.; see Westoby et al. 1992).

Table 1. Fruit-set and average number of seeds per fruit of *P. crassifolia*, in four different populations in three years.

Year	Population	Fruit-set			Seed-set	
		N	Fruits	% fruits/flowers	N	$\bar{x} \pm$ s.d. seeds/fruit
1990	Añisclo I	66	46	69,7	41	7,8 $\pm$ 2,5
	Las Devotas I	274	201	73,4	133	4,7 $\pm$ 2,5
	Las Devotas II	357	285	79,8	40	5,1 $\pm$ 2,0
1991	Añisclo II	297	165	55,5	131	7,5 $\pm$ 3,2
1992	Las Devotas II	338	145	42,9		

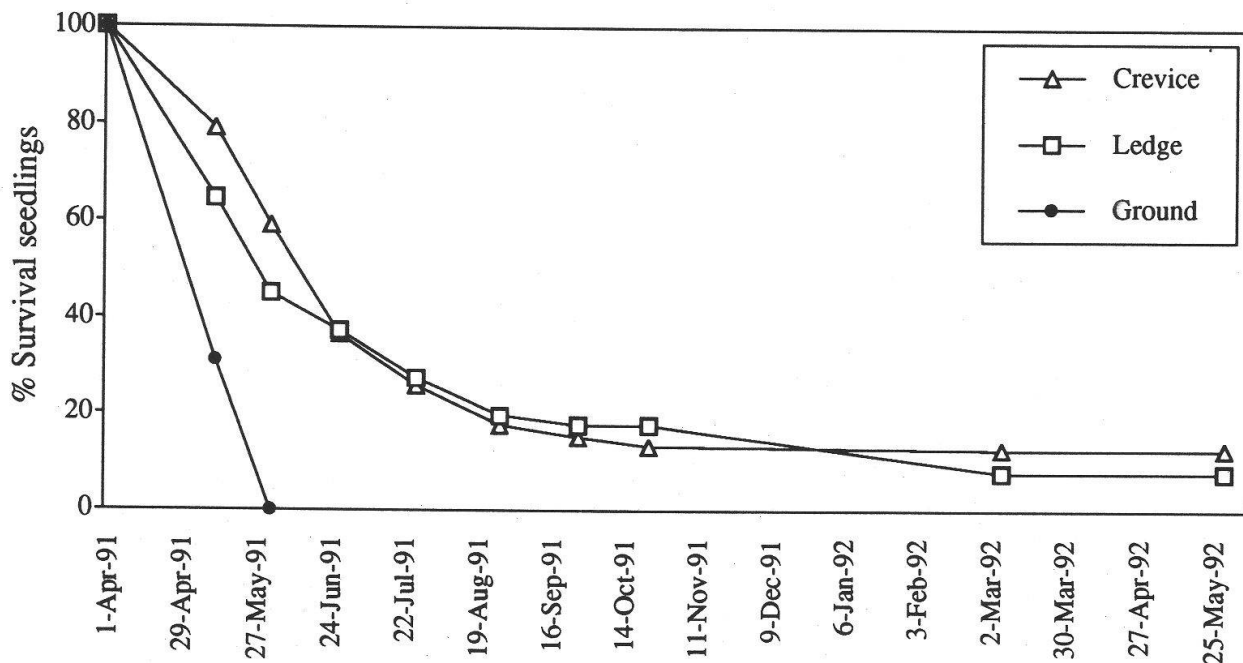


Fig. 3. Percentage of seedling survival of *P. crassifolia* in three different microhabitats during the first year of life.

In some populations throughout the Añisclo Valley, plants located at the bottom of the cliffs (near shrubs) suffered heavy floral predation (up to 100% of the flowers), which entirely prevents seed production. We observed the caterpillar of *Trigonophora flammea* (Lepidoptera, Noctuidae) feeding on flower buds.

### Survival of seedlings

The germination of the seeds takes place early in spring. Seedlings can be seen on the ground, on ledges with some soil, and in rocky crevices. In April of 1991 we marked 242 young seedlings in Añisclo and Las Devotas populations and recorded their microhabitat. During their first year of life they were checked monthly in order to estimate their survival rate.

Spring and summer were the periods with the highest seedling mortality, and survival curves became stable from September onwards (Fig. 3). On the ground all seedlings died in the first two months ( $N=32$ ), and only 10% of seedlings in fissures and on ledges survived the first year ( $N=210$ ).

### Discussion

*P. crassifolia* has some reproductive traits indicating a good adaptation to the vertical and overhanging rocks where it exclusively lives. The incipient pattern of floral zygomorphism of petals and coronal scales provides a small platform that could facilitate visits by pollinators that land on flowers, such as bees (see Stebbins 1970). On the other hand, the movements of the fruits and the myxospermy of the seeds are frequent features in

decreasing dispersal ability, which has been claimed advantageous in habitats where seeds have few suitable places to germinate (Grubert 1974, Ellner and Shmida 1981). These latter traits suggest that founding of new populations must be quite infrequent, because seeds tend to stay near the mother plant.

In addition to the difficulty in placing seeds in favourable microhabitats for germination, most seedlings die during their first year of life, although the estimated 10% of survival during this time is probably a good result, since the year of monitoring was unusually dry. The main problem of *P. crassifolia* seems to be the scarcity of good microhabitats for the development of the species. Floral predation in some small populations also affects reproduction, reducing the number of flowers and therefore the production of seeds. All these characteristics affect the recruitment in established populations negatively.

In spite of its rarity, the reproductive success of *Petrocoptis crassifolia* in terms of fruiting can be regarded as normal since it is similar to or slightly higher than that which plants with hermaphrodite flowers usually have (Sutherland and Delph 1984). On the other hand, by assuming that *P. crassifolia* is a very old taxon (tertiary and subtropical, Montserrat 1979), it seems clear that its survival up to the present is already a success. The most important factor in its survival is probably its ecological specialization, which has allowed it to avoid competition from other, more widespread species which cannot survive in this habitat. In fact, the rock habitats in the Mediterranean region shelter numerous relict taxa, many of which are endemic (Davis 1951, Baudière and Cauwet-Marc 1986). Living in these habitats with weak interspecific competition, *P. crassifolia* shows some limitations associated with its reproduction and dispersal of seeds, problems that it reduces by means of the floral zygomorphism, the moving of fruits toward the substrate, and the myxospermy of the seeds.

At the moment, our results do not indicate that *P. crassifolia* is endangered: its reproduction is good and many of its inaccessible populations escape human and herbivore influences; moreover, most of them are fortunately protected in the Ordesa-Monte Perdido National Park. The limited distribution of the species seems to be fundamentally associated with a great habitat specificity, which usually leads to decreasing competitiveness in other habitats (Drury 1974, Smith 1976), and with a lack of dispersal mechanisms for colonizing suitable but remote habitats (Stebbins 1980).

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