

CONTENTS

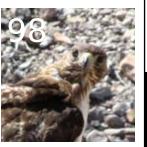


Volume 1 - n° 2

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EditorialSo December has arrived...



Big Bend National Park,
six days in the
Park...



Sempervivum soculense, in the Garda Prealps.



Agave montana, one of the best agaves for the garden.



Honckenya peploides, a succulent on the beach.



Schlumbergera buckleyi, THE Christmas Cactus.



Sempervivum wulfenii, the Sun Houseleek.



EDITORIAL



So December has arrived...

In our Northern hemisphere hemisphere it brings wintertime, with a frost which is even able to make houseleeks dormant, whilst some of them were able to survive millennia of Pleistocene glaciations. A very interesting, succulent genus which is still able to surprise us.

In December it's better to protect our succulents from any winter damage, especially those which grow in our garden. But December is a warm month in many places, even the height of summertime in the Southern hemisphere. Perhaps can we leave for a trip?

In Europe and in many parts of the world, December brings festivities: Christmas.

For most people Christmas is a time for presents, but personally I am reminded of big clusters of epiphytic cacti which I saw as a child; almost completely suberized and covered with pink flowers in December. It was the old, true Christmas cactus, a plant known to our grandmothers, and now almost completely disappeared in many places and substituted by other commercial species of "Christmas cactus". It is sad that this beautiful plant with its high ethnobotanical interest is well known by older people, but young amateurs often do not know about it.

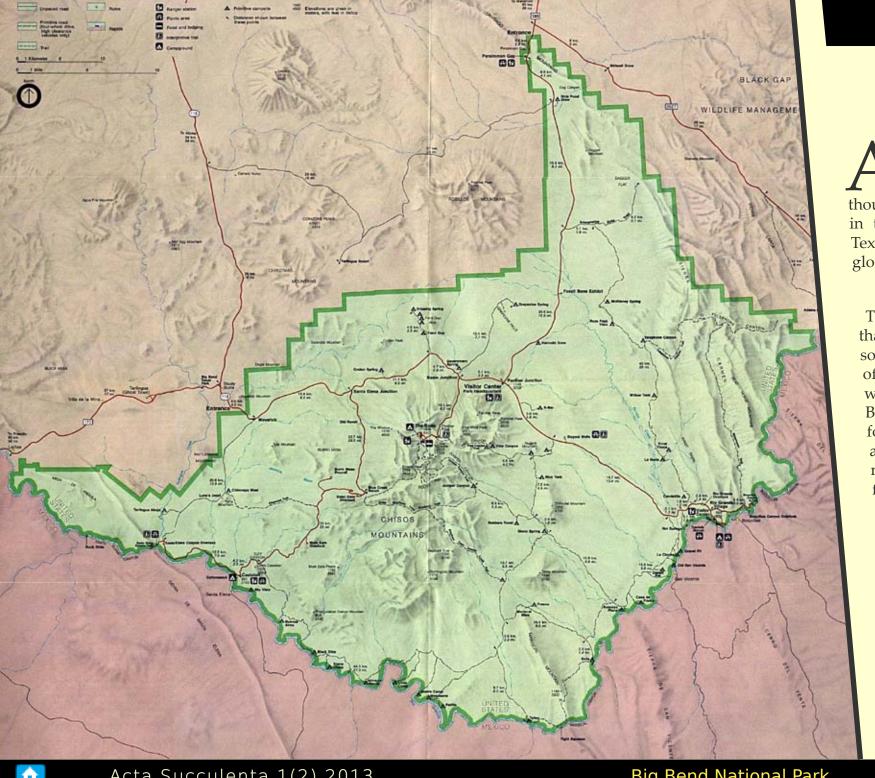
But this December is very special for us: we must thank you.

The welcome to the first issue of Acta Succulenta was excellent and far beyond all our expectations. This only motivates us to continue to do our best in this endeavour.

Thank you all very much.







т the end of March 2010, after 2 weeks spent in northern Mexico, thought about spending some time in the Big Bend National Park, Texas and concluding our trip in glory.

The Park, which measures more than 3,000 km², borders in the south with the Mexican States of Coahuila and Chihuahua, with the Rio Grande (or Rio Bravo as the Mexicans call it) forming a natural barrier for almost 200 km. It is definitely not an impenetrable barrier, for animals and plants at least, since many species can be found on both sides of the border.

South of the Park, in Mexico, the Sierra del Carmen rise, while inside it there's an entire mountain range, the Chisos Mountains.

Immediately to the west there's another Park, the Big Bend Ranch State Park, which is home of the beautiful *Echinocereus russanthus* subsp. *neocapillus*, but visiting this plant requires a certain amount of planning, since it grows in a rather remote place, and apparently a permit is required. Maybe we'll see it another time.

There are two entrances to the Park and we arrived from the west via El Paso, after crossing the border with the US at Ciudad Juarez. We then drove along the Interstate 10 up to Van Hoorn, where we spent the night, and then took the 90 up to Alpine. From here, we took the 118 and headed South, towards the Park.

There's an entrance fee costing \$ 20 for one week.

As you can expect from an American Park, everything is well organized and road signs are everywhere, so a visit is recommended even for the casual tourist.

The majority of the roads inside the Park are unpaved, and for some of them a 4×4 vehicle is recommended, but, after 2 weeks spent in Mexico, I can say all of them proved rather easy. Although our car was an SUV, it wasn't a 4x4 vehicle.



Saturday 20th March

We left the Motel on Interstate 10 at Van Hoorn rather early. During the night it had snowed a little, just a few cm, but it was rather odd to see the desert covered by a white blanket. Three hours later though, when we entered the Park, the snow was gone, although the air was still rather cool.



(Saturday 20th March. continued...)

It took almost one hour to cover the 40 km up to the Visitor Centre, mainly because we stopped often to take pictures of the wonderful desert landscapes, but also because of the relatively low speed limit, 45 mph (70 km/h). This limit is due to the fact that it isn't uncommon to stumble across animals crossing the road, sometimes proceeding in single file, like the Javelina (*Tayassu tajacu*). At the Visitor Centre we collected all maps and information available, and then we proceeded to the Chisos Mountains Lodge, located at about 1700m a.s.l., crossing beautiful landscapes on the way. We stopped along the way for our physiological needs, when, while I was looking at a small clump of *Echinocereus stramineus*, I felt that somebody or something was watching me. A few meters away, some White-tailed Deer (*Odocoileus virginianus* fig.04) were checking my movements. There would be several encounters with these animals during our stay in the Park.

The lodge is the only building inside the Park, and it's obviously often full. I read about this, but since we were two weeks past the Easter holidays, I thought that the peak season was over, but I was wrong. However, at the Reception they gave us some hope that there might be some last-minute vacancies later in the day, so since we had a few hours left before dark, we went hiking along the Lost Mine Trail. Along the trail, beneath the trees, we saw several small clumps of *Echinocereus coccineus* and *Echinocereus dasyacanthus*, none of them in flower unfortunately. When we returned to the lodge, we were told that unfortunately they were still full. Luckily, there was a perfectly serviced camping ground nearby, and we had our tent and sleeping bags with us, so we decided to spend the night there. Unfortunately, the rather good dinner wasn't followed by an equally good night, since our equipment wasn't quite suited for this type of climate, and we were acclimatised to the pleasant warm nights of Mexico, so we passed it shivering in the cold, waiting for the morning sun to warm us up.



Sunday March 21st

After a restoring cup of hot coffee, we dismounted the tent and, firstly, we booked a room in a small hotel just outside the Park, at Terlingua which was a small village that would be our base for our entire stay. Terlingua is famous for its International Chili Cookoff, which is held on the first weekend of November.

After leaving our luggage at the hotel, we returned to the Park, and drove along the Old Maverick Road up to the Santa Elena Canyon. Along the road we saw *Echinocereus dasyacanthus* and *Echinomastus warnockii*, both in flower, as well as *Echinocactus horizonthalonius* and *Coryphantha macromeris*. The Santa Elena Canyon is crossed by the Rio Grande, with one bank on the US, and the other in Mexico. A walking trail, about 2 km long, allows access inside the canyon on the American side.



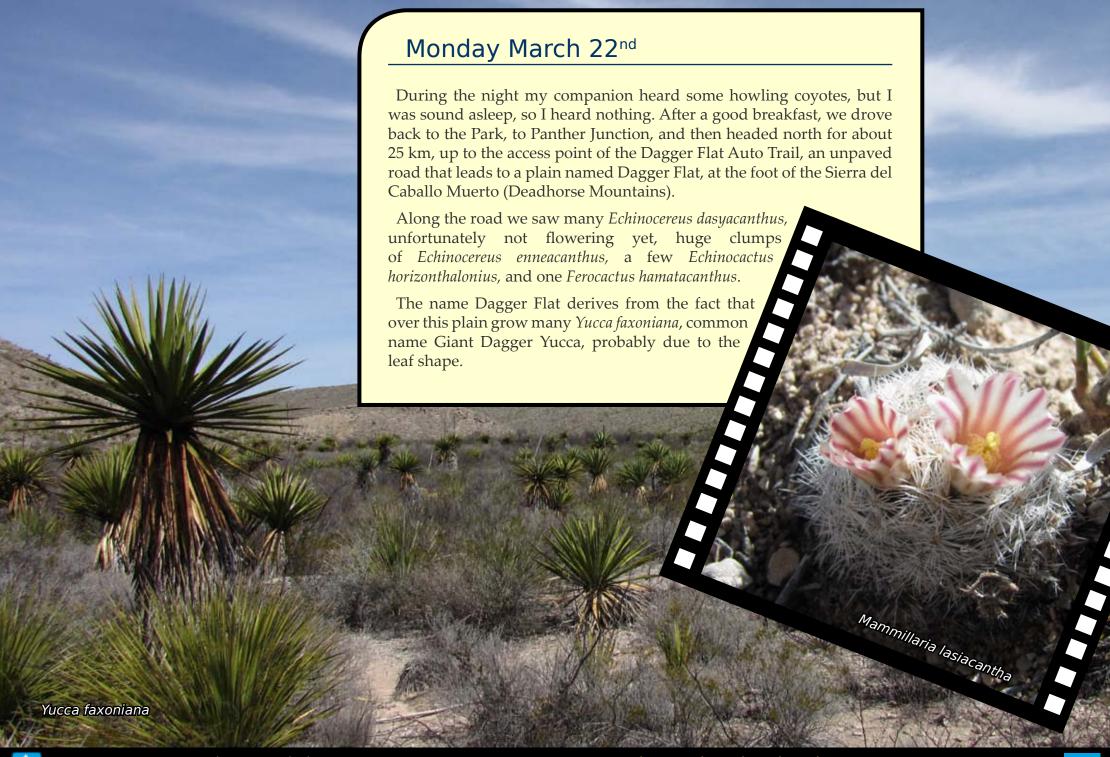
Coryphantha macromeris

(Sunday 21st March. continued...)

We then continued by car a few km to the east, and then north along the Ross Maxwell Scenic Drive, up to the access point of the Mule Ears Trail. This very scenic trail, leads to a spring which is visible at a distance, since it's the only very green spot of the entire area. The spring's name is obviously Mule Ears Spring, and from here you can enjoy a spectacular view of the homonymous mountain. The mountain is just 1193 m high, but is has a very peculiar shape, which from certain angles strongly resembles a couple of mule ears, hence the name.

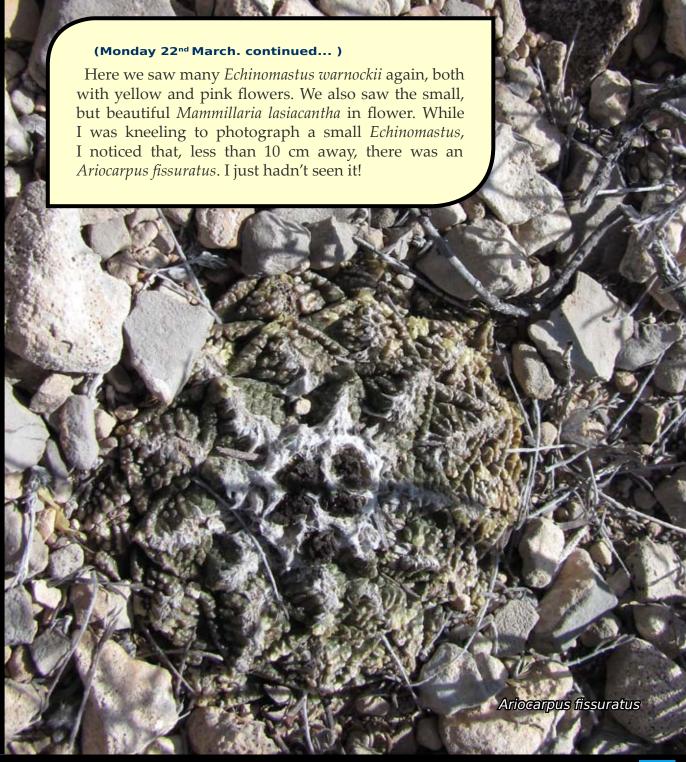


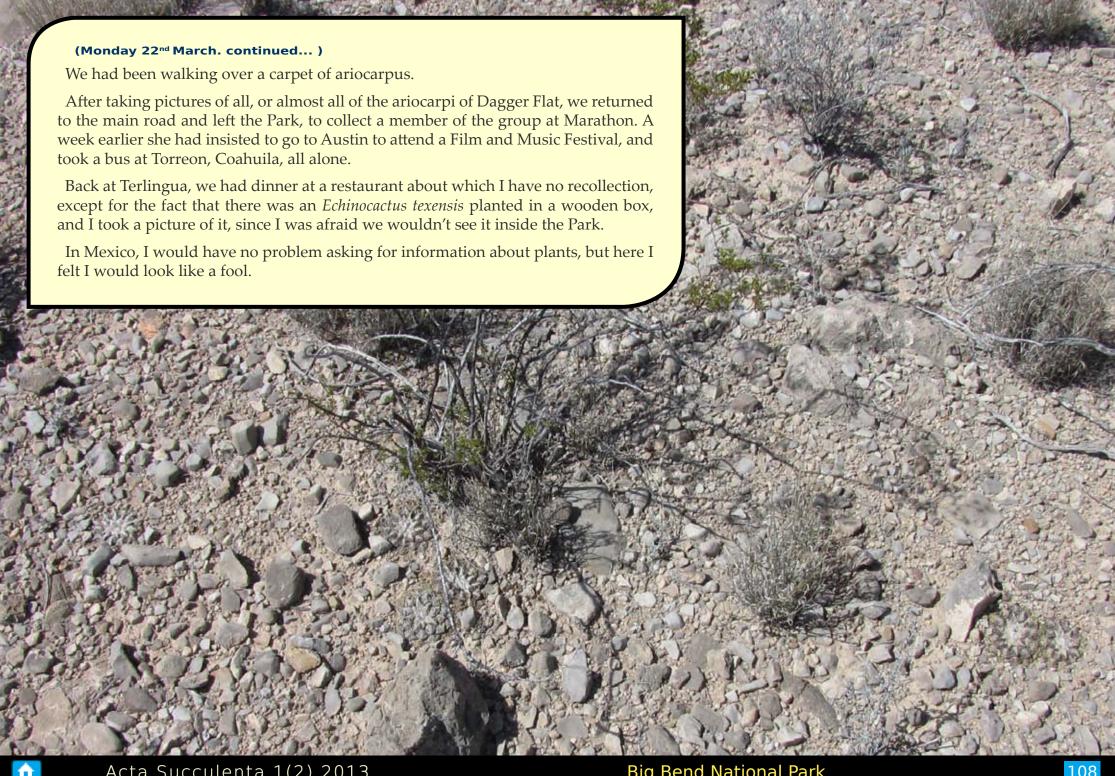












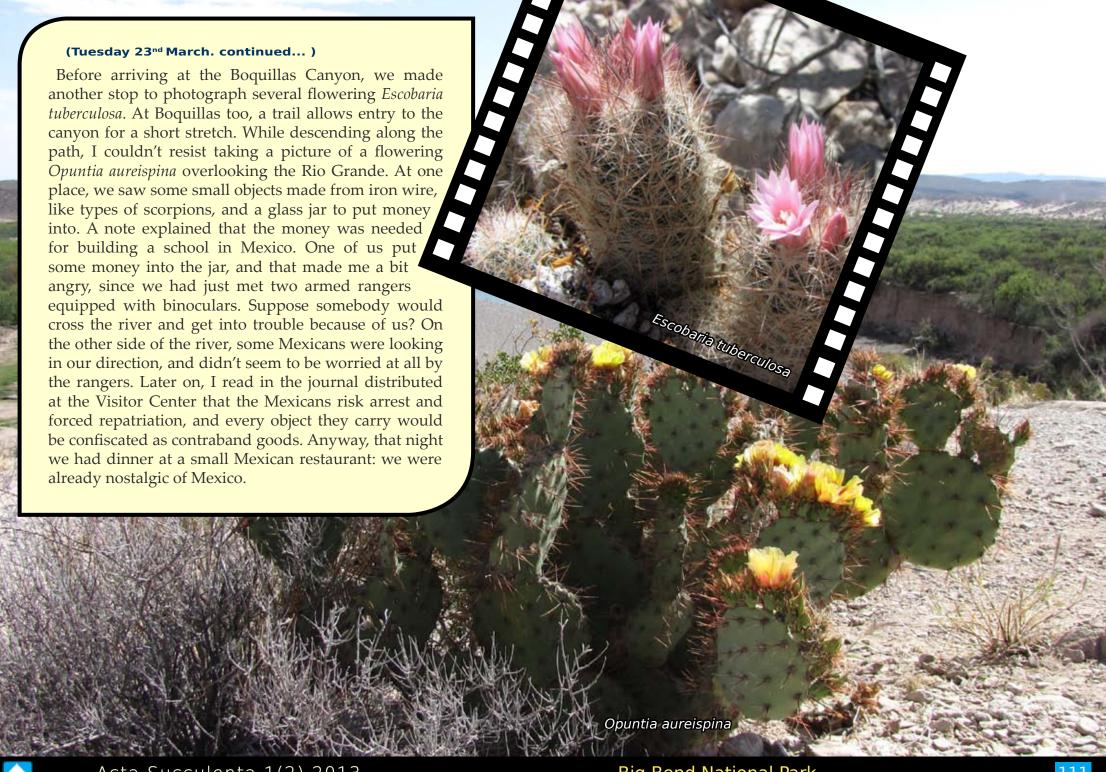
Tuesday March 23rd

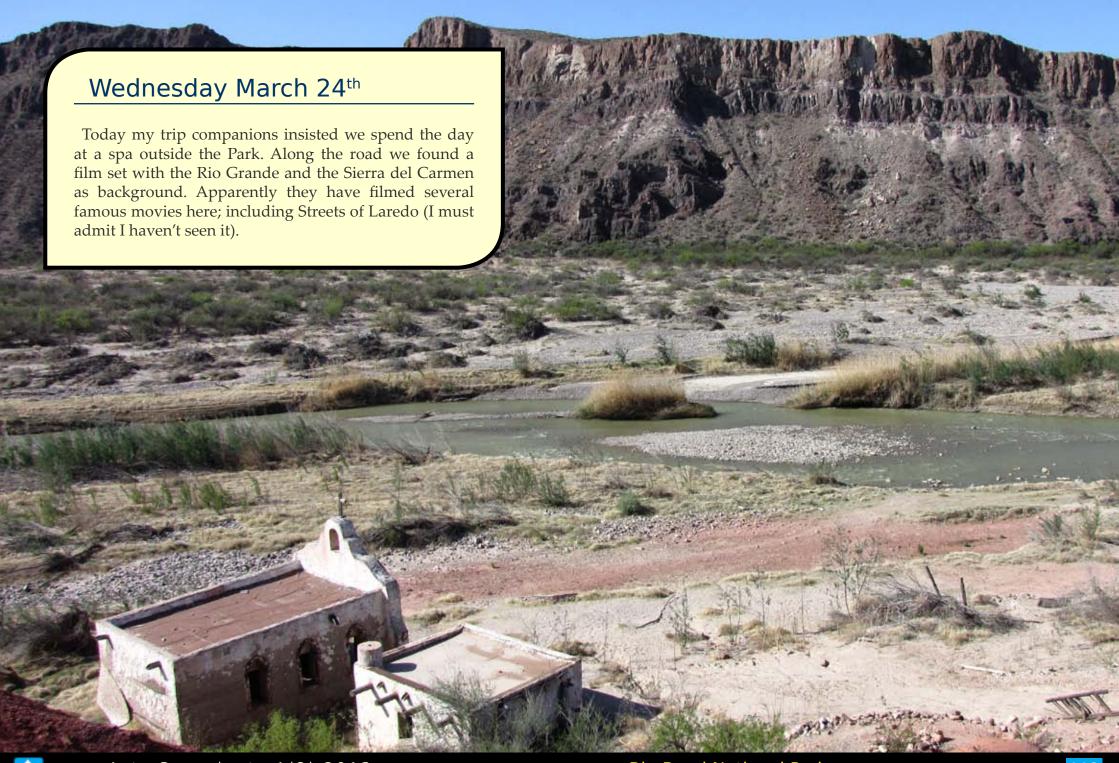
The following day, another unpaved road was awaiting us: the Glenn Spring Road, which is accessed from the main road which from Panther Junction leads to the Boquillas Canyon on the Rio Grande, on the eastern section of the Park. Along the road we saw Mammillaria heyderi, Echinocereus stramineus, Echinocactus horizonthalonius, ubiquitous in the Park, but always with isolated specimens, and again Coryphantha macromeris, another lonely Coryphantha that looked like an echinus, and the usual Echinocereus russanthus, so common that we just ignored it. At a certain point, one of us saw many yellow dots at a distance, and shouted stop! While descending down the escarpment to the right of the road, we saw many Echinocereus dasyacanthus, flowering at last, the flowers having a very rich yellow colour, almost orange sometimes.

I tried to cut open some of the ripening fruits, but every time there was a worm happily feeding in it.



















Summary: Highlighting a new *Sempervivum* species, living as a post-glacial relict in the Garda Prealps: *Sempervivum soculense* D.Donati & G.Dumont sp. nov.; confirming its diploidy by new chromosome counts, and general discussion regarding its integration in the geobotany and phylogeny of the genus *Sempervivum*, and particularly its possible relationship with the tetraploid *Sempervivum tectorum*.

Keywords: *Crassulaceae*, *Sempervivum*, Garda Prealps, Monte Pizzocolo, allopolyploidization, phylogeny, relict.

не flora of the Garda Prealps is characterized by a richness of endemic plants, as well as plants that could be defined as postglacial relicts, that is, plants that have found refuge, during the Quaternary glaciations, in the southernmost part of the Central Alps. Amongst them, we can find a houseleek which although already known, has been neglected, or whose nature has been misinterpreted up to now. In this article we want to give this plant all the importance it deserves, since it can challenge some phylogenetic hypotheses regarding some species belonging to the genus Sempervivum (Crassulaceae), and thus represents a very important element in the understanding of this genus.

Introduction

The Garda Prealps

In Northern Italy, the Garda Prealps are a long mountain range, oriented north-south and encompassing Lake Garda (*Lago di Garda*), from which they get their name. To the West they are delimited by the Giudicarie valleys, to the North by the river Sarca, to the East by the river Adige and to the South by the hills of Brescia and Verona. They can be considered as the southern continuation of the Brenta Dolomite Alps and are separated from the Rhaetian Alps by the Mount Sella di Bondone.

The Garda Prealps can be divided in three massifs ("groups" sensu Marazzi 2005):

- The Giudicarie Prealps.
- The south-western Garda Prealps.
- The eastern Garda Prealps.

From a geological point of view, the Garda Prealps consist entirely of sedimentary rocks: Jurassic grey limestone (Masetti et al., 1998), dolomite limestone, and dolostone (Castellini et al., 2006).

A refuge area for the alpine flora of the Tertiary period

The distinct southern position of the Garda Prealps compared to the rest of the Central Alps (they are basically a promontory wedged in the Padan Plain) has spared some parts of this mountain range from the Quaternary glaciations, and even in ice-covered areas, some cliffs remained ice-free, particularly those facing the lakes. Many plants coming from more northern and higher areas found refuge here during the glaciations. Some of them were then able to completely (or partially) re-colonize their original habitat when the climate became milder, some leaving behind some populations in their refuge areas⁽¹⁾, while others remained confined here⁽²⁾, following the dynamics of each species.

We should point out that the richness and variety of biotopes in this area, and their faunistic and floristic richness, have led to the establishment of various protected areas.

Some species have survived exclusively in these areas next to Lake Garda: i.e Saxifraga arachnoidea Sternb., a relict of the Tertiary period that grows only below rocky outcrops, on a dry substrate, but with high hygrometry (see Reisigl & Keller, 1990).



Amongst the plants presenting relict populations in the Garda Prealps we have, for example, *Saxifraga tombeanensis* Boiss. ex Engl., *Saxifraga vandellii* Sternb., *Daphne petraea* Leybold, etc.

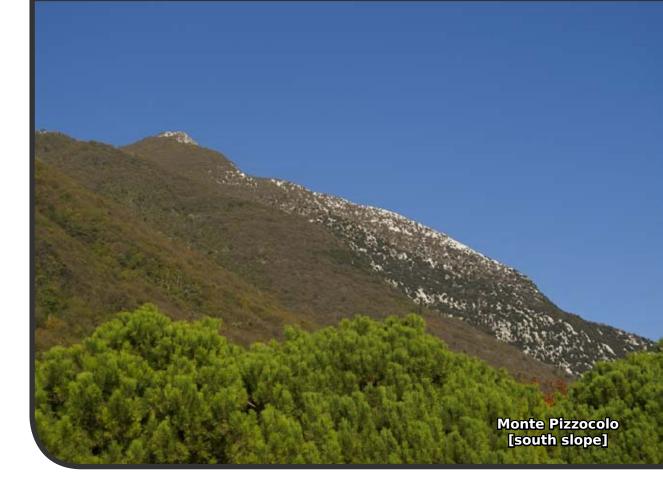
Monte Pizzocolo

Monte Pizzocolo is one of the peaks of the Garda Prealps. It's a very imposing mountain that dominates the southwestern part of Lake Garda, inland to the small town of Toscolano Maderno situated on the lake bank.

Monte Pizzocolo can be defined as a massif of limestone rock, which is particularly compact and sometimes dolomitized and is ivory or beige in colour, arranged in metric layers or even with indistinct stratification, on the eastern flank and near its top. This is the so-called "Corna calcarea" (Zecchini, 2009), a lower-Jurassic limestone, which often shows a pronounced morphology, as the local dialect term "corna", horn, implies. Even if the nearby Monte Spino (1486 m) is mainly formed by "Corna" limestone, the group Spino-Pizzocolo is almost entirely surrounded to the west and to the north by outcrops of Triassic dolostone (Camerini, 2004; Carlini et al., 2010).

The south-western flank and even more so, the lower northern flank of Monte Pizzocolo are densely covered by forests, with rocky meadows (more or less inclined) beginning at 1450 m and reaching right up to the top at 1581 m.

On the contrary, the eastern flank consists of almost vertical cliffs descending directly to the lake. These cliffs are very exposed and mainly consist of naked limestone, well eroded by weather, whilst the vegetation is sparse, particularly in the most exposed areas. On its north-eastern and northern portions, the slopes are very steep, almost vertical in some places and particularly on the northern flank, but this favours higher water availability, so the vegetation is a little denser and it is possible to see plant communities with *Potentilla caulescens* L.



The position and configuration of the eastern flank of Monte Pizzocolo allow us to hypothesize that these cliffs weren't ice-covered during the Quaternary glaciations, or at least part of them weren't⁽³⁾; the part of the cliffs above the glacier which shaped the valley now occupied by the lake.

Monte Pizzocolo is currently located inside a Natural Preserve, the *Parco dell'Alto Garda Bresciano*.

According Corrà et al. (2000), the vertical cliffs to the north and north-east were formed by the erosion of huge glaciers which, according to their theories, could even have split Monte Pizzocolo from Monte Castello di Gaino, which hypothetically formed a single mountain range before the glaciations.

2n = 72

Mitosis of somatic cell (metaphase)
Sempervivum tectorum
[Monte Maddalena]

Karyology and variations within the genus Sempervivum

The genus *Sempervivum* is characterized by an evident general morphologic homogeneity, coupled with a great variability within each species, which can be considered next to each other with relatively undefined boundaries. This genus is probably still undergoing a very active speciation phase and quite often two specimens of the same species look more different that two specimens of two different species. As a consequence, the identification of *Sempervivum* is often difficult, and the current nomenclature poorly and inadequately describes this genus.

Faced with such a situation, one would expect the *Sempervivum* genus to be genetically very homogeneous, and that karyological studies would be of no help in understanding it. Completely wrong. On the contrary, the genus *Sempervivum* is a very variable and complex group from a karyological point of view: the somatic chromosome counts are very variable, starting from 2n = 16 to 2n = 108, with base numbers starting from x = 16 to x = 21 in a continuous succession⁽⁴⁾.

This karyological diversity shows that the genus *Sempervivum* is much less homogeneous that it would seem, and that many taxa are much more separated than their morphology would indicate. For this reason, an exclusively morphological approach to their taxonomy could prove unsatisfactory. Any attempts to solve the above-mentioned complexity of the genus by moving everything into a few large taxonomic frames is as unsatisfactory as exploding the genus into a myriad of mainly useless micro-taxa, since they would represent a simple local ecotype at most, but more often, one of the many levels inside the natural variation range of a single taxon (if not simple phenotypic variations). Unfortunately finding and maintaining an intermediate position is difficult.

The relatively high chromosome numbers and their marked diversity leads one to think that the speciation of the genus *Sempervivum* occurred largely by allopolyploidization⁽⁵⁾ rather than by cladogenesis or anagenesis⁽⁶⁾. For this reason, the study of chromosome numbers is particularly important for this genus, since it allows us sometimes to track or to guess the likely phylogeny of some species or groups of species.

The base number of *Crassulaceae* is considered to be x = 9.

Allopolyploidization is an additive crossing: two not reduced gametes join to form a polyploid individual that is immediately stable and fertile and, if able to sustain itself, will make a new species. AA + BB -> AABB, whereas the result of a simple crossing is AA × BB -> AB.

Speciation is called *cladogenesis* when the original branch splits into two or more branches; it's called *anagenesis* when a species replaces the one from which it derives. In both cases, the chromosome numbers are very often identical in the whole group, hence karyological studies of this group is of little interest.

The Sempervivum tectorum case

One of the most appealing hypotheses for this genus about speciation by allopolyploidization involves Sempervivum tectorum⁽⁷⁾, a widely distributed species in western and central Europe.

Sempervivum tectorum is a tetraploid species with a chromosome number of $2n^{(8)} = 72$, confirmed by numerous different counts. This high number has obviously led to the hypothesis that it could be the result of allopolyploidization between the ancestors of the current Sempervivum marmoreum Grisseb. (2n = 34), a Balkan and Carpathian diploid species, and the current Sempervivum calcareum Jord. (2n = 38), a diploid species from the south-western Alps. In fact, 34 + 38 = 72.

Many factors lead one to consider Sempervivum tectorum as a rather recent species within the Sempervivum genus, certainly more recent that its supposed parents, *S. calcareum* and *S. marmoreum*:

- unlike them, S. tectorum hasn't any evident relict populations that would suggest a Tertiary pre-glacial origin, contrarily to other houseleeks with which it often cohabits (S. arachoideum, S. wulfenii, S. calcareum, etc.). The Monte Pizzocolo population is amongst the few (or the only one?) that could be considered a relict population, but the inclusion of the local houseleek in *S. tectorum* can be questioned, as we'll explain later.
- the distribution range of *S. tectorum* seems to be still expanding westwards, not having reached its potential limit yet; something which is particularly evident in the French Massif Central. This can be deduced by the uneven distribution of *S. tectorum* compared to other, often sympatric species, a difference that can be explained by the later arrival of *S. tectorum* only.



In this article, we consider Sempervivum tectorum L. in its widest sense, that is putting together all the numerous taxa that have been created by splitting this complex and very variable species. The only definition of these taxa is often their geographical location, and they could be sometimes considered at infraspecific level at most, being totally integrated in S. tectorum. In the area treated by this article, we can mention as an example Sempervivum acuminatum Schott non Decne, Sempervivum schottii Baker non C.B.Lehm. & Schnittsp., Sempervivum alpinum Griseb. & Schenk.

The cited articles report on the gametic chromosome count "n" or the somatic chromosome count "2n". We have converted the gametic counts into somatic counts, since in this paper we are using the somatic counts "2n" only. We understand that writing in this way is a relative linguistic abuse for polyploid genomes, but it makes the text easier to read and more understandable when we make comparisons.

A recent alpine origin (Quaternary, post-glacial) of *Sempervivum tectorum* is thus, if not certain, very likely at least.

About the hypothesis of its appearance due to an allopolyploidization mechanism, many factors make it credible:

- The apparent youth of this species, compared to the two diploid species from which it supposedly derives.
- Its high chromosome number, which exactly matches the sum (additive crossing) of these two diploid species.
- Its morphology, that is somehow intermediate between the two putative parents.
- Its strength and ecological plasticity, markedly higher than that of its putative parents, as it happens with the majority of the allotetraploid species, whatever the plant group concerned.

The distribution ranges of the putative parents are presently very distant, but it's possible that they were once very much closer or even overlapped in some places, and were subsequently reduced and separated, disappearing from the central Alps and replaced perhaps by the tetraploid *S. tectorum* in the case of *S. marmoreum* (their current distribution ranges are in contact, but don't overlap). It must also be pointed out that the current distribution range of *S. tectorum* actually links the current distribution ranges of *S. marmoreum* and *S. calcareum*.

This hypothesis is certainly appealing, but it isn't the only one, or at least it could be improved.





Analysis of available data

Monte Pizzocolo hosts a population of a single houseleek species. Its presence has been known for a long time and it's been considered until now, as belonging to the common *Sempervivum tectorum*, omnipresent in the Alps. Some previous studies, which were essentially karyological, outlined its peculiarity, as reported below, but in our opinion, failed to draw the necessary conclusions.

Available data on the houseleek of Monte Pizzocolo

The status of this plant became less clear in 1961, when Zésiger, in a general study on the chromosome numbers of *Sempervivum*, discovered a 2n = 36 number in a *Sempervivum "tectorum"* originating from the "pied sud des Alpes" (southern foot of the Alps), without giving further details about the locality. As all his other chromosome counts of *Sempervivum tectorum*, from various localities (about fifteen), gave a result of 2n = 72, the author apparently neglected this seemingly diploid plant, nor made any hypothesis about it. Zésiger probably considered this odd count was due to an abnormal specimen, with little significance.

After that, Favarger in 1973 again reports a count of 2n = 40 on the same clone of *Sempervivum "tectorum"* (M 552) previously counted by Zésiger as 2n = 36, a result that was confirmed as 2n = 40 by the same Favarger on two more plants (61/926 et 61/927) "récoltées plus tard au même endroit" (collected later at the same locality), again without giving any locality details. This time it was suggested that *S. tectorum* could be sometimes be diploid⁽⁹⁾, adding that a relationship with this plant and *Sempervivum wulfenii* Hoppe ex Mertens & W.D.J.Koch could also be possible.

In 1998 Zonneveld mentions the previous counts and reports a new count of 2n = 38 he made for this population of *Sempervivum* "tectorum", but doesn't say whether it was made on a newly collected clone, or on a previously used clone (probably the latter, since no locality data is given). However, very importantly, he gives its locality at last (undoubtedly after having contacted the previous authors): Monte Pizzocolo. Following the previous authors, Zonneveld doesn't consider this *Sempervivum tectorum* anything special though, except for its diploidy, hence the possibility that the tetraploid populations of *Sempervivum tectorum* (the vast majority) wouldn't be allotetraploid, but autotetraploid, which would challenge the phylogenetic hypothesis of its appearance by allopolyploidization *S. calcareum + marmoreum*.

For many plants, the ploidy level is multiple and variable and it would be a mistake to assign any taxonomic value to it. I.e. Sempervivum arachnoideum can be both diploid (2n = 16) and tetraploid (2n = 32), without showing any differences, so much that even its infraspecific taxa aren't linked by ploidy levels at all. For what concerns the geographical subdivision of the diploid and polyploid lineages, this is very intricate in most of the distribution range. cf. Welter 1977.



About the range of the results

The small difference between the various chromosome numbers (36, 38, 40) should be of no surprise, since counting is technically difficult for the genus *Sempervivum*: it's difficult to obtain good metaphase plates, and their reading isn't very accurate, since the chromosomes of houseleeks are extremely small, punctiform, and so numerous that they often overlap, partially hiding each other. Counting the chromosomes of a houseleek could be compared to counting the marbles which fill a dirty jar from a distance. For this reason, all the chromosome counts published so far should be interpreted as approximate numbers with a variable error margin, directly proportional to the number of chromosomes. Only by repeating the counts over and over, we can arrive at sufficient precision for an individual or a taxon.

What can we gather from these karyological data?

1. - Sempervivum tectorum is really a tetraploid

Due to its vast distribution range, *Sempervivum tectorum* is the houseleek on which the highest number of chromosome counts have been made; practically on plants coming from all the European mountains where it lives. All the counts made on well documented plants have confirmed its polyploidy, except those relating to the population of Monte Pizzocolo.

2. - The Sempervivum population of Monte Pizzocolo definitely seems to be diploid

Subsequent counts, made by different biologists, on different clones, seem to prove that there's indeed a diploid population on Monte Pizzocolo, and it isn't simply an abnormal individual (which could always happen with a single count or even several counts on the same clone in culture).

3. – This population represents the only known case of diploid Sempervivum tectorum

Up to the present, no other chromosome count has ever found a diploid *Sempervivum "tectorum"*, except in this isolated population of Monte Pizzocolo.

4. – There is some doubt about the real nature of this population

In all the cited studies there is no reported field data nor any information about the variability, so that even if it were highly unlikely, we can't exclude beforehand that this natural population could be a single abnormal sterile clone reproducing vegetatively at this locality.

5. - Further data are needed

The case of the diploid *Sempervivum "tectorum"* of Monte Pizzocolo is very intriguing, and the scarcity of field collected data led us to carry out further studies on this plant, *in situ*, in cultivation and in the laboratory.





Materials and methods

Studying the *Sempervivum* populations of Monte Pizzocolo *in situ* has been of fundamental importance, in order to verify its ecology, variability, the actual distribution, as well as the plants that share its habitat, including other houseleeks locally or in the neighbourhood.

We have also collected a few samples of this plant *in situ*⁽¹⁰⁾ (small lateral rosettes) and cultivated them to check their biological cycle and refine its morphological study. The radical tips needed for the chromosome study have been removed from these cultivated clones.

In the lab, the tips of some young and active roots have been cut 3 mm long, and then secured and coloured according to a protocol derived from that of Zonneveld (in litt.):

- 1. immersion is a solution of hydroxyquinoline 0,002M;
- 2. immersion in a solution of pure ethanol (3 parts) and glacial acetic acid (1 part);
- 3. hydrolysis in 5N HCl;
- 4. immersion in Schiff reagent;
- 5. immersion is a solution of K₂S₂O₅ and distilled water;
- 6. squeezing between microscope slide and cover slip and searching by microscope of the best meta-phase plates amongst the mitotic cells, in order to count the chromosomes.

¹⁰ Authorization according to art. 8 of Regional Law n. 10/2008 (Collection of protected spontaneous flora for scientific purposes), by Regione Lombardia - Direzione generale ambiente, energia e sviluppo sostenibile - Parchi, tutela della biodiversità e paesaggio - Valorizzazione delle aree protette e biodiversità.

New data

Field data

Monte Pizzocolo:

The main population of Sempervivum growing on Monte Pizzocolo is located on the limestone of the eastern flank, primarily on the almost vertical cliffs facing east-northeast, and extending up to the north-facing cliff, that could be defined as a vertical rock wall. A few dozen clumps are also present on the steepest points of the south-western flank.

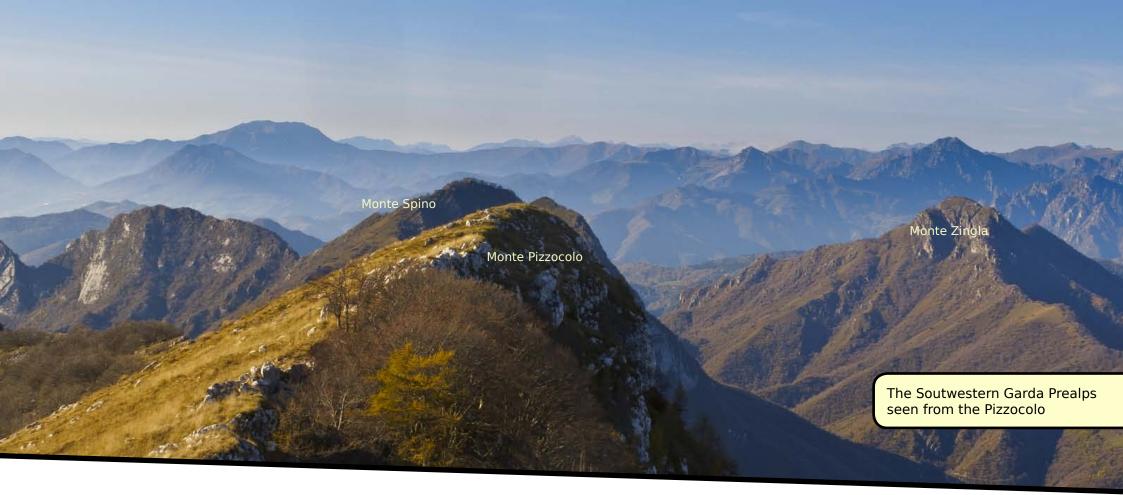
The total population is composed of a single species, the famous "tectorum". No other houseleek has been found.

The majority of the plants are concentrated starting from about 1450 m a.s.l. up to the mountain top, although some clumps can be found starting from about 1350 m. The scarcity of plants on the rocky meadows near the top is maybe linked to the plant's ecology (preference for habitats in rupicolous situation), as the current concentration on steep or almost vertical rocky cliffs would suggest. It's also possible that the presence of a World War I fort on the top first, and the trampling by many tourists later (Monte Pizzocolo is a favourite destination for excursionists due to the fantastic panorama that can be enjoyed from the top) have reduced its presence on the summit meadows to a few sparse clumps, leaving most of the plants concentrated in less accessible areas (the almost vertical cliffs).

The plants grow directly in rock cracks or on rocky protrusions where a little humus and clay have accumulated and allowed the establishment of various types of rupicolous vegetation.

We verified that the population of Pizzocolo shows an evident morphological variability between the individuals, which can eliminate the above-mentioned hypothesis that it could be a single clone reproducing locally and vegetatively.





Surroundings of Monte Pizzocolo:

All the peaks and passes near Monte Pizzocolo (Monte Spino, Monte Zingla, Monte Carzen, Passo di Tremalzo) have been visited to check the presence of other houseleeks. This search was unsuccessful; we did not find the plant or any other houseleek.

The *Sempervivum* populations nearest to Pizzocolo can be found on Monte Maddalena, near Brescia, on one side, about 16 km distant as the crow flies, and on Monte Baldo, on the other shore of Lake Garda, on the other side, again about 16 km distant as the crow flies. These two populations consist exclusively of *Sempervivum tectorum*, and lack any morphological peculiarities. Another houseleek that can

be found nearby, eastwards from Monte Baldo is *Sempervivum globiferum* subsp. *hirtum* (L.) 't Hart & Bleij⁽¹¹⁾, but that belongs to the subgenus *Jovibarba*, a distinct group whose members don't hybridize with true *Sempervivum* (subgenus *Sempervivum*).

Sempervivum globiferum subsp. hirtum represents a very wide taxonomic group, which includes morphologically very variable populations, very difficult to separate, unless an infinity of micro-taxa with little importance is created. The local form near of Monte Baldo has been recently differentiated as Sempervivum globiferum subsp. lagarinianum (Gallo) Stephenson, its definition mainly relying on a chorological criterion (isolated population on the southern boundary of the distribution range) rather than on ecological and morphological criteria: the debate about the taxonomical value of this taxon is still in progress and it's outside the scope of this paper, so we prefer here to keep the classical combination as above.

Description

Clump: not copious, with few daughter-rosettes, isolated rosettes flowering without having produced any daughter-rosettes aren't rare. Stolons are short, barely exceeding the diameter of the mother-rosette. As generally happens with *Sempervivum*, no stolons are produced during the year in which the rosette flowers, which occurs after a vegetative phase of several years (monocarpic rosettes).

Adult rosette: rather large, diam. 6-10 cm, exceptionally up to 20 cm; number of leaves variable depending on the individual (25-50+); symmetrically arranged leaves without any evident anisophylly⁽¹²⁾. During the vegetative phase, the central leaves are often arranged like a cone, particularly at the end of the growing season (an inconsistent and variable character).

Leaves: wide lamina, with rather marked mucron; glabrous blades; non-glandular cartilaginous marginal cilia, densely and regularly arranged. A nice, often strongly glaucous colour, particularly at the beginning of the growing season and before flowering; many specimens show, especially on younger leaves, an alternation of paler, glaucous transversal bands and darker, greenish ones; basal blotch from cherry red to purple, more or less pronounced and clear, but relatively constant with good exposure; the blotch has indistinct margins gradually blending with the leaf's glaucous colour. A clear apical blotch is missing, but some specimens with a good exposure can show a light beige apical blotch, small and scarcely evident, mainly at the beginning of spring. Whenever present, the apical blotch is always less evident than the basal one.

Inflorescence: flower stalk tall, sometimes taller than 60 cm, hairy-glandular, with a "minaret"-like structure, that is, a tall stalk bearing many but short subequal lateral branches, distributed along the stalk. Such a stalk's morphology is rather rare in *Sempervivum*, occurring with good frequency and evidently only in *Sempervivum calcareum*. The stalk shape of this houseleek clearly differs from the common shape of the stalks of *Sempervivum tectorum*, including the populations of *S. tectorum* nearest to Monte Pizzocolo (Monte Baldo). The typical flower stalk of *S. tectorum* is markedly three-branched at the apex, whilst further down, there are a few lateral branches of decreasing importance (acrotonous branching), whose number and importance varies depending on the stalk's vigour.

Flower: large and markedly polymerous (often more than 12 subdivisions); greenish petals, pale and with a slight pinkish basal blotch (actually consisting of thin and short pink stripes on a whitish background), with a hairy-glandular external blade; reddish staminal filaments contrasting with the greenish petals.

Possible identifications: although this plant has been linked with *Sempervivum tectorum* up to now, in our opinion it more resembles *Sempervivum wulfenii*, both in situ and in cultivation, and it's not easy to determine at first glance whether it is one or the other, especially during the vegetative phase.

Anisophylly is the difference in shape and size between leaves located nearly at the same level on an axis, hence with comparable age and function. Anisophylly frequently occurs in houseleeks in the vegetative phase during the growing season, *Sempervivum tectorum* being one of the species where this occurs more frequently and evidently.







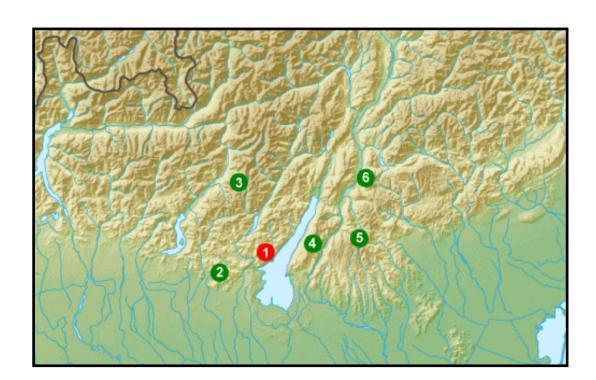


Karyological data

We have performed new chromosome counts on this plant by using new clones we collected *in situ*, hence of known origin, and almost certainly different clones than the ones used in previous counts (see above).

Our results confirm the previously published data: this plant actually has a **diploid genome** and the somatic number we count is **2n** = **38**. Since the quality of the meta-phase plates was rather good, the error margin should be low.

Our data agree with previously published counts (2n = 36, 38, 40), so we can consider the *Sempervivum* population of Monte Pizzocolo as truly diploid, with somatic chromosome number 2n = 38.





We have also checked the chromosome numbers of the populations of *Sempervivum tectorum* nearest to Monte Pizzocolo, following an almost elliptical orbit around it. Again, we have used material collected by us in habitat, and followed the same counting method we used for the Pizzocolo plant. 1

- Monte Maddalena (Brescia): 2n = 72
- 3 Proximity of Passo di Croce Domini (Brescia): 2n = 72
- 4 Rifugio Telegrafo, monte Baldo (Verona): 2n = 72
- **5** Campobrun, Lessinia (Verona): 2n = 72
- 6 Forte Dosso del Sommo (Folgaria, Trento): 2n = 72

As the data indicate, we have found no diploid individuals and all the specimens were tetraploid.



Our chromosome counts can be checked through video files which we made at the same time. In viewing frame by frame, it is possible to change the focus as if you have your eye on the microscope. To perform an accurate count, you will need a graphics program managing layers and stack into it some snapshots of the video or, more simply, use transparent plastic sheets placed on the screen.

These video files are freely available under Creative Commons BY-NC-ND 3.0 license on the website of the journal (http://acta-succulenta.eu) or directly from the authors.



Discussion

At present, no tetraploid individual has been found amongst the Monte Pizzocolo population, after various counts on several specimens (clones). We are thus really in front of a true diploid population.

In addition, no diploid Sempervivum tectorum has ever been found in the proximity of Pizzocolo or in any other locality. This is definitely a unique and isolated diploid population, located in a place recognized as a shelter-area for some Tertiary species during the Quaternary glaciations. A tetraploid can easily stem from a diploid, but not vice-versa: we can then suspect that this is a relict population, a residual testimony of an ancestral population, that was once perhaps more widespread in the central Alps.

The inflorescence morphology compares to that of Sempervivum calcareum from the southwestern Alps, and its chromosome number is identical too (2n = 38). This latter species has been, until now, the only known true houseleek (subgenus Sempervivum) with this chromosome number, all the other houseleeks belong to the subgenus Jovibarba, and are very different plants⁽¹³⁾, with no direct parentage link with *S. calcareum*, so their matching chromosome number is certainly a coincidence.

All these karyological, morphological and chorological data make us doubt that the population of Pizzocolo represents a typical Sempervivum tectorum.

Starting from that premise, we can then examine five different hypotheses to understand this plant:

Hypothesis 1: it could be a Sempervivum tectorum, if not a typical plant, at least an intra-specific taxon

Hypothesis 2: it could be a very ectopic relict population of *Sempervivum calcareum*.

Hypothesis 3: it could be a relict population of *Sempervivum wulfenii*.

Hypothesis 4: it could be an ancient (more or less stable and fixed?) hybrid between Sempervivum tectorum and a now extinct species from Monte Pizzocolo.

Hypothesis 5: it could be a new species, overlooked and mis-interpreted up to now.

The separation between subgenus Sempervivum and the subgenus Jovibarba is clear and there are no species with intermediate characters between the two. Actually, many authors consider Jovibarba as a separate genus, but we prefer to treat it as a subgenus for reasons to which we shall return because they go beyond this article.





<u>Hypothesis 1</u>: *Sempervivum tectorum*

This *Sempervivum* population, up to now considered belonging to *Sempervivum tectorum*, is rather isolated and, as we mentioned above, morphologically well distinguished from the nearest *Sempervivum tectorum* populations, since the latter don't show any difference compared to the typical *S. tectorum* morphotype of the central Alps. Furthermore, the chromosome number of this population (diploid 2n = 38) differs from that of the nearest *Sempervivum tectorum* populations, as well as from those that have been counted so far (tetraploid, 2n = 72).

Could this isolated population be the testimony of an ancestral diploid status of Sempervivum tectorum, that would then be an autotetraploid rather than an allotetraploid, and could this autotetraploid have replaced in the entire distribution range its diploid ancestor, now present only on the shelter-station of Pizzocolo? We can't rule that out completely, but it's rather unlikely: first of all because the autotetraploid would have lost two pairs of chromosomes, a significant loss, but this loss would also have happened homogeneously throughout the entire vast distribution range of *S. tectorum*; something difficult to imagine, since the appearance of autopolyploidy is very likely polytopic and diluted in time. We shouldn't also forget that although an allotetraploid is generally stronger and ecologically more adaptable compared to the diploid parents (due to its double genome), this strength is very rare in autopolyploids. An autopolyploid is often a victim of the expression of recessive defects and its fertility is usually lower⁽¹⁴⁾ than the diploid from which it derives⁽¹⁵⁾. It can be observed that an allopolyploid can easily replace one of the diploids from which it descends from, but an autopolyploid generally tends to cohabit with the original diploid as a simple "chromosomic race" here and there, without any tendency to replace it, and never completely. Hence, the hypothesis according to which the Pizzocolo's houseleek would be an ancestral diploid form of Sempervivum tectorum and that the latter is autotetraploid (with chromosome loss) seems highly unlikely. Even more so, if one considers the morphological peculiarity of the Pizzocolo population compared to Sempervivum tectorum as it is in the rest of the region and throughout its distribution range.

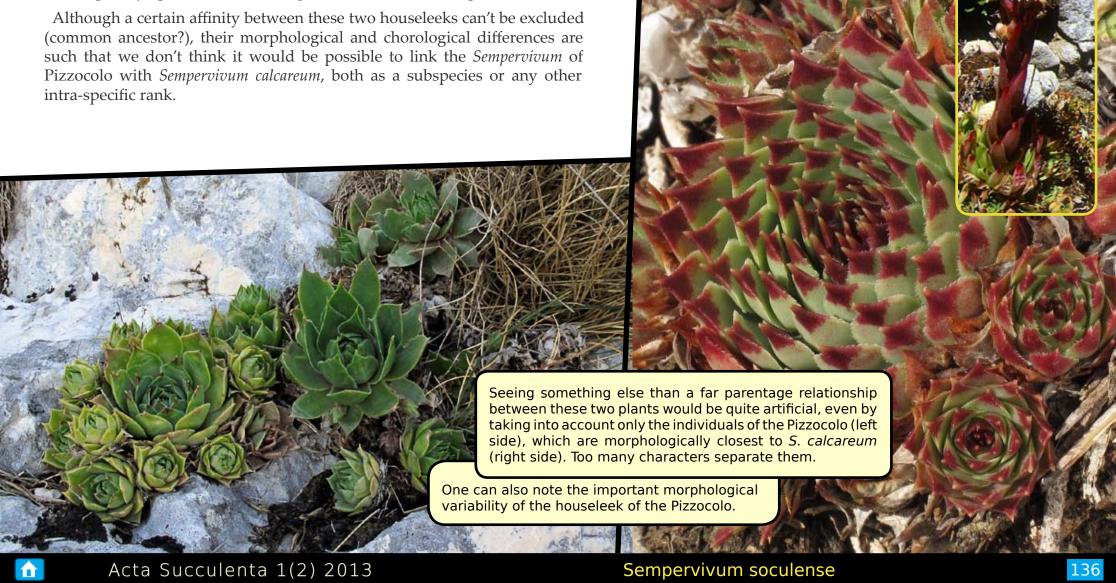
For this reason, it's not possible, in our opinion, to continue considering the Pizzocolo plant as *Sempervivum tectorum*.

¹⁴ Quadrivalents formation instead of bivalents in chromosomal pairing, during meiosis.

Mind you: all these statements refer to the result of polyploidy, not its mechanism: the spontaneous **auto**polyploidy of a diploid hybrid produces an **allo**polyploid actually, but this mechanism is rare compared to the creation of an allopolyploid by non-reduced gamete crossing.

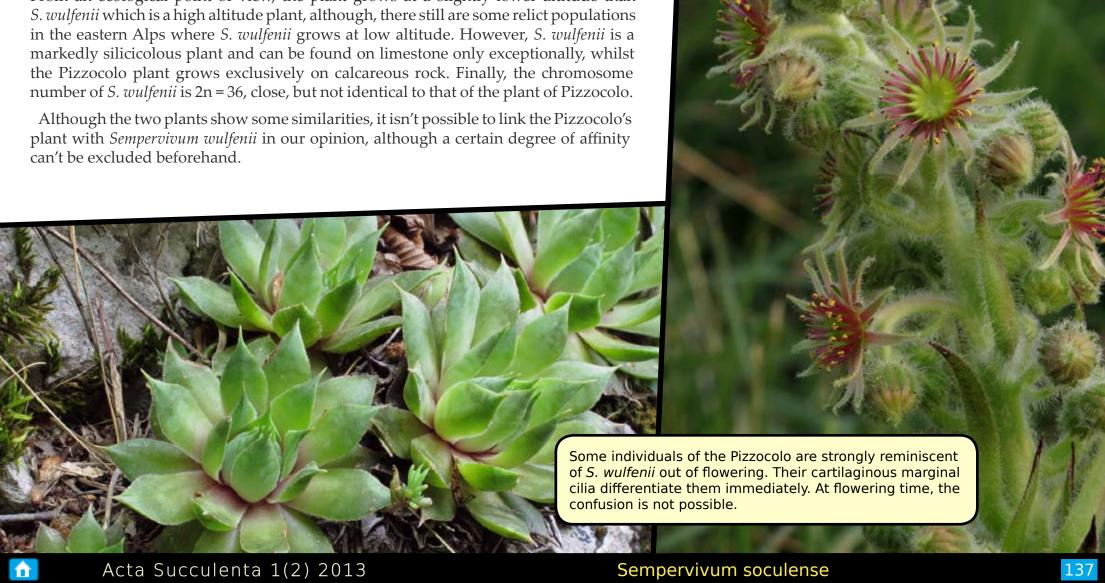
Hypothesis 2: Sempervivum calcareum

As already reported, the Pizzocolo houseleek shares some characters with *Sempervivum calcareum*, that is, its chromosome number and the very peculiar morphology of its flower stalk. However, the distribution range of *S. calcareum* is very far (the limestone south-western Prealps) on the other side of the Alps, and never crosses the ridge line. Moreover, the Pizzocolo houseleek lacks many distinct and constant characters of *S. calcareum* (very numerous, rigid leaves, prickly apex, "raisin" looking old leaves, flowers shape, etc.).



Hypothesis 3: Sempervivum wulfenii

The wide, glaucous leaves with a red basal blotch, but lacking the apical one, and the erratic presence of a leaf cone, can remind one of *Sempervivum wulfenii*, a species located a little more to the north and north-east, in the Rhaetian Alps. Rather than with *Sempervivum tectorum*, it's the resemblance with this species that comes to mind when observing the plant of Pizzocolo *in situ*. However, the inflorescence of the latter is clearly different, as is the flowers' shape; in addition, the marginal cilia aren't glandular (a very important character for the identification of *S. wulfenii*, although not every evident). From an ecological point of view, the plant grows at a slightly lower altitude than *S. wulfenii* which is a high altitude plant, although, there still are some relict populations in the eastern Alps where *S. wulfenii* grows at low altitude. However, *S. wulfenii* is a markedly silicicolous plant and can be found on limestone only exceptionally, whilst the Pizzocolo plant grows exclusively on calcareous rock. Finally, the chromosome number of *S. wulfenii* is 2n = 36, close, but not identical to that of the plant of Pizzocolo.





Hypothesis 4: hybrid

Hybrids are very frequent amongst houseleeks, and often dominant in certain natural populations, even replacing the parent species in some cases. The identification of a *Sempervivum* should always take into consideration that it might be a hybrid.

The pale flower with thin and numerous greenish-white petals, the glabrous rosettes with an inconspicuous or often missing apical blotch, the inconstant presence of an apical leaf cone; all this would be compatible with the aspect of a *Sempervivum tectorum* × *wulfenii* hybrid, a plant known for being difficult to distinguish from *S. tectorum*.

The somatic chromosome number of such a hybrid (tectorum 2n = 72) × (wulfenii 2n = 36) is 36 + 18 = 54, would be quite different from 38, but, by backcrossing with S. wulfenii we would get 27 + 18 = 45, a number closer to 38. However, to explain a somatic chromosome number of 38 starting from 45, we would have to introduce some meiotic anomalies in the hybrid, enough to force the loss of three pairs of chromosomes, which would be far, far too much. We would also have to expect a very dis-homogeneous hybrid population, with a high variability of chromosome numbers (not the case here), in which the triploid component having a chromosome number close to 40 would be one amongst others, very likely showing marked sterility (not the case here) being a triploid. Hence, we can exclude the hypothesis of the hybrid population between S. tectorum and S. wulfenii.

From a morphological point of view, we could also hypothesize a possible ancient hybridization of *S. tectorum* with a now defunct member $^{(16)}$ of the complex group *Sempervivum zeleborii* (2n = 64), but it should be rapidly discarded, since the theoretical somatic chromosome number of such a hybrid would be 32 + 36 = 68 and its backcrossing would still maintain a very high chromosome number.

This now eastern group of yellow flowered houseleeks, was once certainly distributed over the Alps, since a vestigial population (*Sempervivum pittonii* Schott) is still present in the Austrian Prealps.



Implications and consequences

Nomenclatural consequences

All the data reported above lead us to consider that the identification of the houseleek of Monte Pizzocolo as *Sempervivum tectorum* is an error, and that this plant is really a new, unknown species, which we describe as follows:



Sempervivum soculense D.Donati & G.Dumont sp. nov.

Sempervivum, **rosula** magna, symetrica, 6-10(-20) cm diam.; **foliis** valde mucronatis, glauco-viridibus, basi obscure rubra, apice rare leviter colorato, glabris, margine ciliis brevibus eglandulosisque, externis patulis, centralibus nonnumquam conice condensatis; **stolonibus** rosulae contiguis, saepe paucis, nonnumquam absentibus; **caule florifero** alto usque 60 cm vel ultra, glanduloso-piloso, non acrotone successive breviter ramoso; **floribus** breviter pedicellatis, plus minusve 12-partitis saepe ultra, petalis virido-albidis basi roseole leviter lineolatis, filamentis rubentibus.

A Sempervivo tectorum atque S. wulfenii, praesertim caulis habito et chromosomatico statu, a S. wulfenii insuper ciliis, differt.

Habitat in Italia septentrionali, in Alpibus benacensibus, in calcareis saxosis cacuminis clivorumque montis Soculi (Pizzocolo).

Holotypus a nobis designatus : leg. D.Donati & G.Dumont, n° DDGD13A, 2013-11-28 ; « Versante NE del monte Pizzocolo, Toscolano Maderno, Brescia », 1580 m s.m. ; in herbario bononiense (BOLO 507977) depositur. Isotypus in herbario florentino (FI).

NB: the protologue of this taxon is represented by the Italian edition of Acta Succulenta.



Relationship with Sempervivum tectorum

The fact that we consider *Sempervivum soculense* as a distinct species from *Sempervivum tectorum* doesn't mean that, in our opinion, it doesn't have any relationship with it. The only peculiarity of our point of view is that we don't see it as a progeny, but as an ancestor of the latter.

In our opinion, *Sempervivum soculense* could be considered as a direct descendant of the diploid plant having led to *S. tectorum* by allopolyploidization.

As reported above, the isolation of *S. soculense* on Monte Pizzocolo leads one to think of a post-glacial relict; that this plant or its direct ancestors were populating the central, and perhaps the eastern Alps at the end of the Tertiary period. Regarding *Sempervivum marmoreum*, this was probably populating, at it does now, the Balkans and the Carpathians, but maybe the eastern Alps too.

The most likely scenario is hence thus:

During the Quaternary glaciations, the distribution of *Sempervivum soculense* was squeezed southwards, reduced to some rare ice-free mountainous areas south of the Alps, with the wide Padan Plain blocking its further descent to the south and with a possible redistribution northwards between glaciations; one of these shelter stations was Monte Pizzocolo.

On the contrary, *Sempervivum marmoreum* had all the space it needed to regress towards the Balkans, where it's still abundant even today. No obstacle opposed its moving back, unlike *S. soculense*.

When the post-glacial climate became milder, the two plants gradually re-colonized the ice-free alpine areas and connected (or re-connected) themselves. Being inter-fertile⁽¹⁷⁾, hybrids were formed; by accident, some of them were allotetraploid additive hybrids, they are what we call today *Sempervivum tectorum*. This has in turn rapidly and totally replaced its two parents throughout its expanding distribution range, occupying the same ecological niche, but with a higher competitivity and ecological amplitude in case of cohabitation⁽¹⁸⁾.

Some cases of allotetraploid plants that have rapidly replaced the parent plants can be observed even by using human life as a time scale. One of the most spectacular and well known cases is that of *Spartina anglica* C.E.Hubb, an allotetraploid, that in a few decades has almost entirely replaced its diploid parent *Spartina maritima* (Curtis) Fernald in every area where they cohabited. It's even likely that in a few decades the parent plant could become extinct, except in some rare residual stations where the tetraploid hasn't yet arrived, or where it's regularly cleared out to preserve *S. maritima* and its environment (see Lacambra 2004).



We haven't tested the interfertility between *S. soculense* and *S. marmoreum* in cultivation, but this can almost be taken for granted, since all the houseleeks belonging to the subgenus *Sempervivum* are more or less inter-fertile, so much that when a hybrid between two sympatric species is missing *in situ*, this is a symptom of the hybrid's scarce competitivity, rather than the consequence of a sterile crossing. The proof of this is that it's very easy to obtain hybrids in cultivation which are unknown in the wild.

This hypothesis seems chorologically more likely than the one that considers *S. calcareum* as one of the parents of the allotetraploid *S. tectorum*.

Therefore, *Sempervivum tectorum* has most likely replaced most of the ancient populations of *Sempervivum soculense* and the survival of this relict population on Monte Pizzocolo can only be explained by its isolation and the fact that *S. tectorum* hasn't colonized this mountain, at least not yet.

Amongst the possible explanations of the failed colonization of Monte Pizzocolo by *Sempervivum tectorum*, topography and geology have probably played a major role:

- As already mentioned, Monte Pizzocolo is surrounded by dolomitic rocks. Due to their richness in magnesium, dolostones are inhospitable substrates for many plants, including most houseleeks: *S. tectorum* is one of them, very common on the central Alps, on limestone and crystalline rocks, but absent or very rare on dolomitic rocks, which are quite frequent in this area of the southern central Alps. The only houseleek that grows on dolostone in this part of the Alps is a rare and localized species, *Sempervivum dolomiticum* Facchini, absent in the area near Pizzocolo.
- Lake Garda, a sort of small inland sea, represents an insurmountable barrier to the east and to the south of Pizzocolo for *S. tectorum*, despite the fact that it grows on the opposite side about fifteen km away only, as the crow flies. This impassability is enhanced by the fact that the enclosed and elongated shape of this big lake channels the winds in a north-south direction and vice-versa, blocking a possible transportation of the seeds by the wind from one shore to the other.

The theory that *Sempervivum tectorum* is a descendant of *Sempervivum soculense* (or more exactly its direct ancestors) by allopolyploidization, although it remains a hypothesis, is surely not pure botanical fiction because it seems to be backed-up with serious arguments.



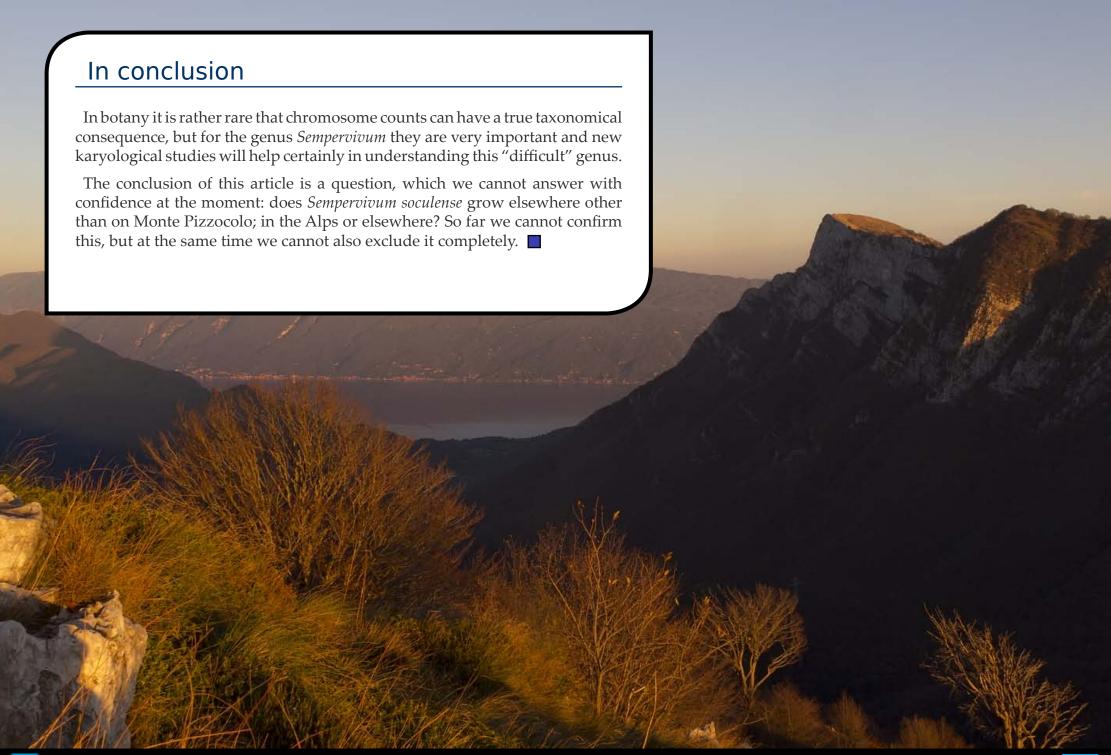
The future of this plant

The unique, known population of *Sempervivum soculense* exists inside a Natural Preserve (Parco dell'Alto Garda Bresciano) where collecting or destruction is forbidden. Furthermore the collection, damage or the destruction of houseleeks is forbidden in the Lombardia Region by Art. 8 of the regional law n. 10/2008. So the plant is well protected by the local administration. This plant is also protected by its ecology, since it grows mainly in very dangerous places, barely accessible by trekkers, a fact which limits any trampling threat.

Nevertheless, the number of individuals on Monte Pizzocolo is quite limited⁽¹⁹⁾ and the species is presently unknown elsewhere. This strict endemicity in a single massif, without any possibility of expansion, makes *S. soculense* potentially vulnerable: whilst it doesn't need a further protection, careful and regular monitoring will be very useful.



The total number of specimens is hard to define, due to the difficulty in exploring the northern vertical slope, but we can estimate them to be several hundred, though surely not several thousand.





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- to Prof. **B.J.M. Zonneveld** for his valuable advice about chromosome counts and their application to the genus *Sempervivum*.
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In recent times, the succulent garden has become very popular, particularly in regions apparently not adapted to xerophytic plants, such as in central Europe, or in areas where the climate is Continental or quite humid and cold. Here it is possible to enjoy amazing *Yucca*, *Dasylirion*, many *Cactaceae* and other succulent plants.

The challenge of frost hardy succulent gardening

These gardens are the consequence of the courage of many "brave" gardeners, who along the years have read almost all the literature available about hardy succulents and then applied this knowledge in their gardens. There were many disappointments, because the frost resistance of many plants is not fixed, but is connected to the local climate, so that the higher the hygrometry and the pluviometry, the lower is the frost resistance of a succulent or xerophytic plant. If most xerophilous⁽¹⁾ plants don't like an excess of water even during the growing season, many xerophytic plants, for example *Yucca* species, love frequent watering during the warm months. On the contrary, the majority of frost hardy succulents are hard pressed to endure a humid or rainy climate during the autumn and early spring months, when the temperature is not frosty but is still cold: their suffering is evident and they show damage and fungal disease.

So the efforts of these brave "succulent gardeners" were enormous and rich in disappointments, but after many attempts, they selected a list of plants from the dry tropics which are able to survive the vagaries of the climate of the temperate zones; in many case thanks to various tricks.

In this list, the agaves are among the stars.

¹ Xerophilous means "which loves (and needs) aridity"; Xerophytic means "which is able to grow in arid environments"

Agaves, their beauty and their problems

Have you ever been in central Southern Italy (but Southern Spain, Southern France, Greece, etc. can do as well), close to the sea? Whilst they are endemic to central –North America, with a maximum concentration in Mexico; in Southern Europe agaves have become naturalized, and majestic specimens of *Agave americana* L., *A. titanota* Gentry, *A. ferox* K.Koch, *A. sisalana* Perrine ex Engelm., etc., are found, some taller than a man and forming enormous clusters on the slopes and cliffs down to the sea.

Unfortunately, the majority of the species (generally the most beautiful) are truly xerophilous and very sensitive to humidity and excessive watering (or rainfall in our case) during the cold months.

So are beautiful agaves a dream anywhere else other than areas with a Mediterranean climate? They aren't, because some species (a few, if the truth be told) can survive or even grow well under other climates, with the right tricks.

One of them is surely *Agave montana* Villarreal⁽²⁾.

² Agave montana Villarreal, in Sida 17(1): 191-195 (1996). Type: leg. Villareal & al., n° 8120, 1995-05-05; « MÉXICO. Nuevo León: Municipio de Rayones, cima de la sierra de la Marta, 42 km al E de San Antonio de las Alazanas, 25°09'N, 100°23'W, ..., 3,300 m »; Holo. MEXU, Iso. ANSM ENCB.



Agave montana

Can you imagine an agave which lives even above 3000 m asl, grows in dense pine forests, receives a lot of snowfall every year and looks like a sort of hybrid between *Agave utahensis* Engelm. and *A. victoria-reginae* T.Moore (nice enough to go crazy), but is much bigger?

This plant is *Agave montana*: it is found in the Miquihuana area, on the border between the Mexican States of Nuevo León and Tamaulipas. Its habitat is in the upper reaches of mountains, generally above 2000 m to 3200 m asl, and consists of dense pine forest, where the plants grow in clearings or even under the trees. The climate is quite humid, and the vegetation is vigorous with heavy rainfall during the warmer months. Snowfall is not rare in wintertime, due to the high altitude.





The most vigorous plants grow where the conditions are more humid, and in these places the rosettes consisting of a large number of leaves can grow up to 1.7 m wide and 1.2 m tall, and the inflorescence can reach 5 m or more in height. The plants which are well exposed to sunlight tend to be pale green to occasionally yellowish in colour, whereas the plants which grow partially shaded, at least for part of the day, have a dark green colour with whitish stripes, which reflect the impression of the teeth of the younger leaves which pressed against that position (the leaf imprint). The above mentioned teeth and the apical spine are very robust and are reddish-brown in colour. The immature floral stem is impressive with its violet colour, and the flowers are yellow.





How to grow Agave montana in our garden

The ecology of this plant, combined with its beauty, as reported above, should make it one of the best agave options for a xerophytic garden in a temperate climate.

This statement is only partially true.

We should never forget that in its natural habitat, even in the worst case, the soil needs quite a few days or at least 1-2 weeks to dry out, and the water never sits in the core of the rosette but dries very quickly.

In colder, more humid climates, the soil can remain damp or even wet for many months, but above all some water can still remain among the leaves at the centre of the rosette for weeks, and this is a very bad thing, particularly if it freezes during the night and liquefies in the day time. These conditions can damage even the hardiest of the agaves, the much trumpeted Agave utahensis, which can die within few weeks in these conditions. A. montana could probably survive all winter (not always) but the damage will be evident.

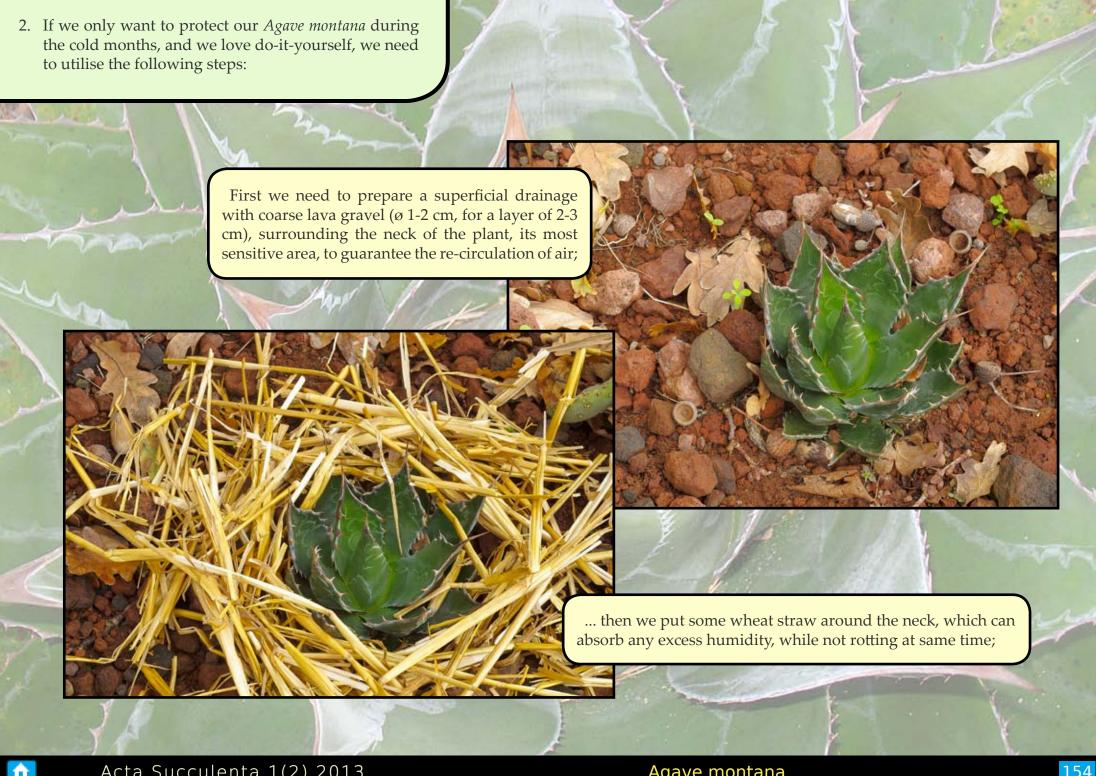
We need some tricks.

First, we need to prepare a rich but very well drained soil for our agave. A commercial soil for cacti should be fine and we should fill a large hole (ø 50 cm) which we have prepared in the garden, whose depth should be at least 50 cm, since the root system of the agaves is huge and very expansive. The best time to transplant agaves is the late spring, so that the plant has enough time to establish itself before winter.

When the colder months are due, we have three possibilities to help our agave to survive:

1. If we have a very well drained flowerbed where we grow it among other succulent plants, we can just cover it with a homemade plastic tunnel. This will protect all the plants from rainfall and humidity and the greenhouse effect will warm the environment during any sunny winter days. In this way A. montana is frost hardy to -15°/-20°C, but this method has a problem: if the tunnel is not big enough, the still, humid air can promote fungal pathogens.

















Softhem share the same biotopes as tourists, namely the beaches! They also share many other environmental factors with these bipeds, such as heliophily and the same optimal growing period: the summer months. The main difference between the beach plants and the bipeds is that the first are unable to live elsewhere; cohabitation is hence not always easy...

Among these daughters of the sea, one of the prettiest is surely *Honckenya peploides* (L.) Ehrh., the 'Sea Sandwort'. It's also or more exactly, it would be, one of the commonest on the ocean beaches... if it would be allowed to live in peace.





Ecology

Honckenya peploides, together with Cakile maritima Scop. (the 'Searocket', another succulent plant, from the Brassicaceae family), a few *Atriplex* spp. (mainly *A. laciniata* L., non-succulent, from the Chenopodiaceae family), and, less abundantly, Salsola kali L. (the "Prickly saltwort", a spiny succulent Chenopodiaceae) and a few other scarcer plants, forms a very particular plant community: the community of the upper beaches from the Atlantic temperate areas of the northern hemisphere.

Further north, *Honckenya peploides* is still present and abundant and is associated with some other plants such as Mertensia maritima (L.) Gray (the famous 'Oyster-plant'), and participates in the Arcto-boreal upper beach communities.

The upper beach, a very peculiar biotope

The "Upper beach" must be understood not as the backshore or the foot of the dunes but as the upper part of the beach itself, which means the upper part of the intertidal zone (the zone where the tides move back and forth). The so-called upper beach is the zone covered by the tide only during the Spring-tides(1) and remains uncovered during the Neap-tides (following a cycle of two weeks associated with an equinoxial cycle) excepted during storms. Depending on the profile of the ground, the angle of the swell and the local tidal range, this upper beach zone can spread out from a few metres to tens of metres wide⁽²⁾.

Depending on the energy level of the waves in the area, the boundary between the upper and lower beach can be more or less marked by a change in slope.



In fact, the upper limit of the upper beach is above the theoretical level of the high tides because it varies greatly depending on the weather: The sea rises significantly higher in conditions of low pressure than in conditions of high pressure and clearly exceeds the upper beach during stormy high tides.

Lower down on the beach, the water covering is constant twice a day with the tides, and even if this area remains uncovered during a part of each day, it belongs to the marine domain. It's the irregularity of the water covering which makes the upper beach what it is and makes it a border zone, swinging ceaselessly between the marine domain and the terrestrial domain.

Most tourists have the idea that a beach consists of sand, possibly some pebbles, and nothing else, except for a few cigarette butts and oily meat roasting here and there. This completely wrong conception is maintained by managers of sea-side resorts, who struggle to regularly "clean up" their beaches, thereby completely eliminating the particular flora of the upper beaches.

You must therefore visit some unmanaged beaches which are more isolated and un-crowded to realize how much the appearance of most beaches is unnatural by the man-made arrangements, excessive tourism and the regular but destructive "clean ups". A sandy or gravely beach is a natural environment like any other, with its fauna and flora, and a few higher plants have succeeded in colonizing the particularly harsh environment that is the upper beach and to make it their living environment. One of the most characteristic among them is *Honckenya peploides*, which is also a true succulent.

Typical, relatively unaltered, aspect of a sandy upper beach with *Honckenya peploides* on the Atlantic coast:

- 1: high tide marks (organic debris deposited by the sea)
- 2: dense mat of Honckenia peploides
- 3: Honckenya peploides emerging after being buried.
- 4: embryonic dune with *Elymus farctus*
- 5: foot of the white dune with Ammophila arenaria

The upper beach, a very hostile biotope

For a plant, the upper beach is a very hostile environment, which means an environment where establishing and surviving are difficult, for the following reasons:

- It's a dessicant environment with a dry substrate, even in areas with high rainfall. Indeed, the narrow coastal strip receives less rainfall than the inland and the evapo-transpiration of plants is intense, despite the high hygrometry, because of the almost constant wind linked to the phenomenon of thermal breezes⁽³⁾. The sandy substrate is very porous and retains the water for a few hours at most, and only tens of minutes for the surface layer in summer. The bigger the grain size the faster the drying. In addition the sun exposure is constant all day long (no shade, very loose vegetation), which increases the drying of the surface of the substrate and of the plants. The plants must therefore be heliophilous and must develop effective strategies for capturing and saving water: thick cuticle, succulence, roots diving deep down into the wet deeper layers wet for some (Cakile maritima for instance) or, conversely, a dense superficial and extensive network which can capture every drop (this is the case with *Honckenya peploides*).

- It's an environment with a very soft substrate in which plants struggle to anchor themselves firmly. Plants must hence develop morphologies and adapt different growth patterns: long taproots diving very deeply to anchor in the most stable soil layers (it's the strategy of Cakile maritima) or a dense horizontal network of branching stems below the surface which root at the nodes and thereby stabilize the substrate (it's the strategy of Honckenya peploides). Already mentioned above as adaptations to the dryness of the substrate, it is clear that these morphological adaptations of the underground organs are not unequivocal.

The ground is warmer than the sea during the day and cooler at night. This difference creates thermals and a thermal wind which alternates twice a day: the sea breeze during the day, the land breeze at night.



- It's an <u>environment with a very mobile substrate</u>. The sand drifts with the wind, tides and currents, continually changing the profile of the upper beaches. Plants must be able to tolerate a partial uprooting and, *above all*, a regular burial. They must be able to quickly emerge from the sand that covered them, regardless of its thickness, by producing not simple etiolated stems but stout and fast-growing vertical shoots and quickly recovering their aerial morphology when they emerge from the sand. In practice, one observes that upper beach plants take advantage of regular burial which, far from disturbing them, on the contrary stimulates their growth and helps their anchorage in the ground.

- It's a <u>mechanically aggressive and abrasive environment</u>. Plants of the upper beach are at the forefront during offshore storms. Strong winds can break and pull the stems or uproot plants, and the sand carried by the wind exerts a very strong abrasion of their epidermis⁽⁴⁾. During the largest tides, plants are often more or less submerged and subject to the powerful mechanical action of waves breaking onto the upper beach and to the abrasion by various suspended solids in the water (sand,

small pebbles, etc.). Plants must hence develop systems to resist these attacks, a direct resistance (mechanical strength, flexibility, low-growing habit, aerodynamic and hydrodynamic tufts) or an indirect resistance (fast regrowth from the rootstock).

- It's a <u>very saline environment</u>, rich in chlorides (sodium chloride, NaCl, mainly). The upper beaches are regularly visited by the tides and therefore subject to massive salt intake. The salinity is high, but it is also *very* variable and *brutally* variable with the tides flooding the substrate, then the rain washing and desalinating the surface. The sea spray also causes a quasi-permanent salt deposit on the epidermis of plants, resulting in severe leaf burn if the plant is not adapted. As for the continuous deposition of salt on the ground by the spray, it is the main cause of the permanent salinity of the environment, as the salinity brought by tides is larger but much rarer and more sporadic. The presence of salt increases the effective dryness of the substrate by creating a high osmotic pressure which must be overcome by the plant in order to be able to absorb water by its roots. One again, the succulent morphology is an asset in this fight against salt, allowing it to accumulate high osmolarity vacuolar contents.



Try to walk during a stormy day at the foot of a dune: you will not stand long, and your skin will remember painfully the impact of each micro-grain of sand (a few hundred thousand per second...) and then you will understand the aggressive power of sand... and punishment that the plants suffer! For them, it's even worse because most of the movement of sand takes place in a layer 30 cm above the ground.

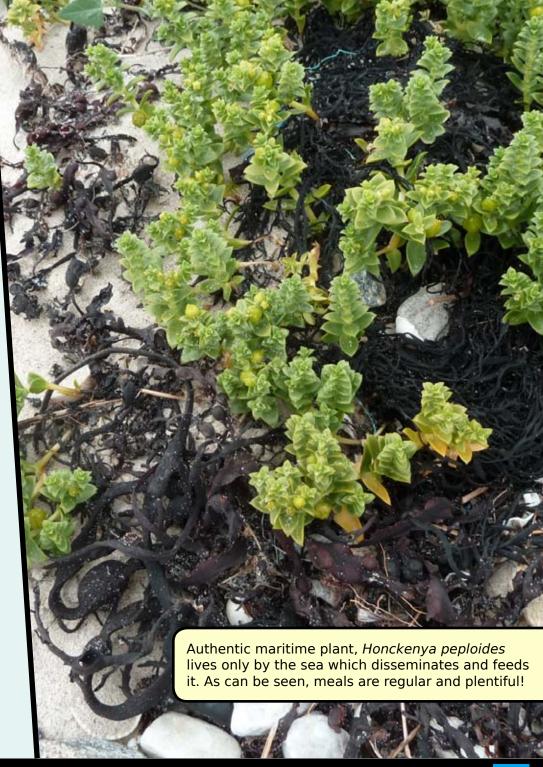
- It's a <u>dynamically unstable non-permanent environment</u>, as subject to an annual cycle of sedimentation/erosion⁽⁵⁾ and is *totally* destroyed at varying intervals by heavy storms. Plants growing there are hence *all* pioneer plants; this name refers to plants able to establish themselves and to colonize a totally pristine environment and to do so quickly. The peculiarity of such an environment is that it can remain perpetually in the immature stage of alternating colonization/destruction without ever stabilizing and evolving to subsequent stages.

- It's is a <u>highly anthropic environment</u>. The upper limit of the upper beaches is often very developed, disturbed, concreted, covered by riprap (rocky breakwater) or flattened, and always overcrowded during the summer. The movement and exchange of sand between beach and dunes is therefore more and more difficult, plants are trampled and, worse, coastal municipalities have stated that with regard to the plants on the sand "That doesn't look clean". Some dreadful mechanical devices have therefore been developed to mix and sift the sand by removing any trace of life of it.

- It should be noted however that if the upper beach is a very hostile environment for the establishment of plants it's not because it's a poor environment, despite appearances. Indeed, the upper beach is regularly enriched with plenty of organic matter by the debris line⁽⁶⁾. This debris is quickly buried under the sand by the wind and provides all the required minerals and nitrogen supply to the plants. Plants adapted to such environments, at the same time rich in salt and rich in nitrogenous substances are called halonitrophilous.

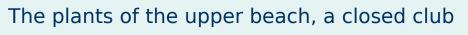
The normal dynamics of the beach-dune sedimentary system is that the beach loses sand in winter: this removed sand accumulates in the subtidal zone (the foreshore under the water) and the dune goes back and opens in places. The dynamic is reversed in the summer and the upper beach recharges itself with sand and secondarily supplies the dunes by wind.

The high tide marks are composed of debris carried by the waves and deposited at each tide at the upper limit of the high tide; this debris draws thick brown edging lines on the upper beach. Debris consists mainly of organic matter (varied small dead animals, algae, etc.) and, alas, now some plastic... This debris shelters abundant specific microfauna which causes quick a degradation and recycling of organic matter, except when an abusive "cleaning" breaks this cycle; this disastrous practice does indeed not only destroy any flora and fauna of the upper beach but it also removes any possibility for them to establish themselves. Without the debris



lines the upper beach is a sterile environment and subject to accelerated erosion.





In such an environment, only tourists feel good! ... Tourists and a very few plants such as *Honckenya peploides* and its companions mentioned above⁽⁷⁾.

7 It must be remembered that the little world of the upper beach also includes many arthropods which are strictly confined to this environment and even some birds that pest there in late spring (Charadrius alexandrinus)



The very low number of species in the plant communities of the upper beach demonstrates how hostile this environment is and how difficult it is to colonize and indicates therefore how the plants that inhabit it are highly specialized. If you try to count the species present on the upper beach of a given beach, you only need one hand! This very small number of species profits to the rare plants that have succeeded to adapt to such conditions: they have little competition to face, or rather "they had"... The plant communities of upper beaches had succeeded over millennia to adapt themselves to the worst possible conditions, but facing Man, his shoes and his machines, the fight has been too unequal and gradually they have left the scene and are now only a memory on many beaches...

Honckenya peploides





Living at the beach all year round!

Among the plants of the upper beaches of the western Atlantic temperate zone, only *Honckenya peploides* is actually perennial⁽⁸⁾. Therefore it faces the winter there, while its most usual companion, Cakile maritima, although biennial or short-lived perennial, behaves as a strict annual on the upper beaches, and all the Salsola and *Atriplex* spp. are true annuals.

Most plants of the upper beach zone have adopted an attitude of escape, in order to combat the difficulty in colonizing this environment throughout the year: they relocate there every spring then disappear during the following autumn. On the contrary, Honckenya peploides survives the winter and its storms, even though it is badly damaged and seems to disappear. The main parts of its stems are destroyed by equinoxal storms but most, or at least large pieces, of the network of its rootstock spends the winter buried in the sand and gravel and resumes its growth vigorously in the first fine days.

Another perennial also adventures rather frequently on the upper beach, Beta maritima L., but it is much less associated to it and being extremely nitrophilous, it is found mostly in sheltered areas where organic deposits are abundant, coming from the sea or the land. The few other perennials sometimes encountered on the upper beach (Matricaria maritima L., Polygonum maritimum L.) plants are rather plants from the embryonic dune and the fore-dune and also prefer shelteredand protected areas.



Its domain: the beach and only the beach

Honckenya peploides is therefore defined ecologically as a perennial psammophilous⁽⁹⁾ halonitrophilous xerophyte, characteristic of the upper beaches. In the temperate zone, its usual habitat is more or less coarse sand or sand mixed with gravel, even the base and the maritime side of the pebble bars because its perennial nature requires a minimum of substrate stability during winter storms. Further northwards in its vast natural area it is also common to find it in most stony or even rocky environments.

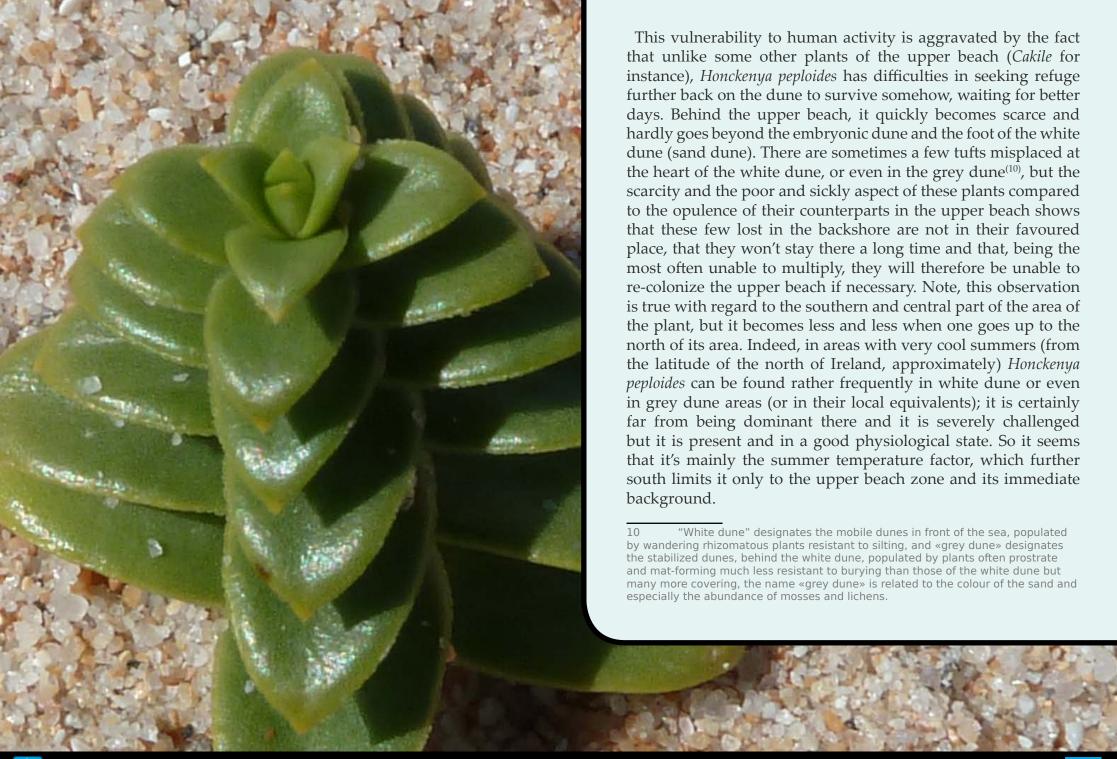
A fairly common and characteristic habitat consists of areas of bare pebbles during the winter which is then covered by a layer of sand in the summer. There the plant finds the stability which allows it to withstand winter storms and the soft substrate allows it to run its summer growing stems in all directions.

In its most characteristic habitat in the temperate zone which is sand, more or less stabilized by pebbles, *Honckenya peploides* can produce uniform mats covering a considerable area, provided that the beach is hardly used by people because, although it withstands salt and drought as well as the violence of the wind and the sea, its juicy foliage cannot resist long term trampling and even less beach "cleaning". A tuft occasionally trampled could easily recover from its underground stem network but if trampling recurs the plant will disappear quickly. Regarding the passage of the screening machine, the first passage is final: the network of rhizomes and roots being rather superficial, nothing will grow again after that...

^{9 &}quot;Psammophilous" = "sand loving", term for plants growing in the sand. When Latin roots are preferred to Greek roots, one can use "sabulicolous" or "arenicolous" = "living in the sand". These three terms are equivalent but the first is the most used. Some authors provide a nuance to these terms, reserving the term of psammophile to plants of mobile sand and sabulicole to those of stabilized sand.









Stay and propagate

The multiplication of *Honckenya peploides* is both vegetative by its dense network of rhizomatous stems, and sexual. Its seeds are ripe from late July and, less abundantly, until mid-September and beyond; they are rather large and light, they float and are dispersed by the water as well as by the wind. Carried by the waves, they arrive on beaches with the debris of the high tide mark, in which they germinate. Stem fragments broken by storms can be transported in the same way and then easily take root in the sand, a few roots being already present at nodes near their base. *Honckenya peploides* is therefore a thalassochorous⁽¹¹⁾ plant.

Compared to plants of the upper beach which have an annual cycle, the natural seedlings of *Honckenya peploides* are very scarce⁽¹²⁾ and it seems clear that its vegetative propagation is largely predominant *in situ* and that most of its large mats have a clonal origin, not really monoclonal but made up of a small number of individuals.

Thalassochory refers to the phenomenon of dispersion of a living organism by the sea. For a plant, this dispersion may be vegetative (fragments or complete individuals uprooted then stranding) or sexual (seeds floating projected by spray or deposited in debris lines). We have already discussed this mechanism in *Acta Succulenta* 1(1) about *Crithmum maritimum* L.

At least, they *seem* scarce because they are very difficult to differentiate from young stems emerging in the spring out of the substrate.

Honckenya peploides plays a significant role in the dynamics of dune systems. Indeed, it stabilizes the sand of the upper beach with its dense network of creeping stems below the surface and, more importantly, it accumulates in its mats the sand brought by the wind, creating embryonic micro-dunes, some of which may evolve into true white dune in areas where the coastline tends to move forward; then *Honckenya peploides* will be replaced by plants characteristic of the white dune⁽¹³⁾. All the plants of the upper beach have this ability to create embryonic dunes but the observation *in situ* shows that one of the most effective plants able to trap sand is often *Honckenya peploides* because of its habit of creating wide mats bristling with lower stems.

In the European Atlantic area, these plants are mainly the marram grass Ammophila arenaria (L.) Link or, further north, the sea rye Leymus arenarius (L.) Hochst., the dune blue thistle Eryngium maritimum L., the sand spurge Euphorbia paralias L., the dune bindweed Calystegia soldanella (L.) Roem. & Schult. etc. Some plants are more specific at the dune foot, establishing a gradual transition between the vegetation of the upper beach and that of the white dune (or what replaces it), with a foot in both worlds, one of the most characteristic is the very common sand couch-grass Elymus farctus (Viv.) Runemark ex Melderis, sometimes confused with the marram grass.

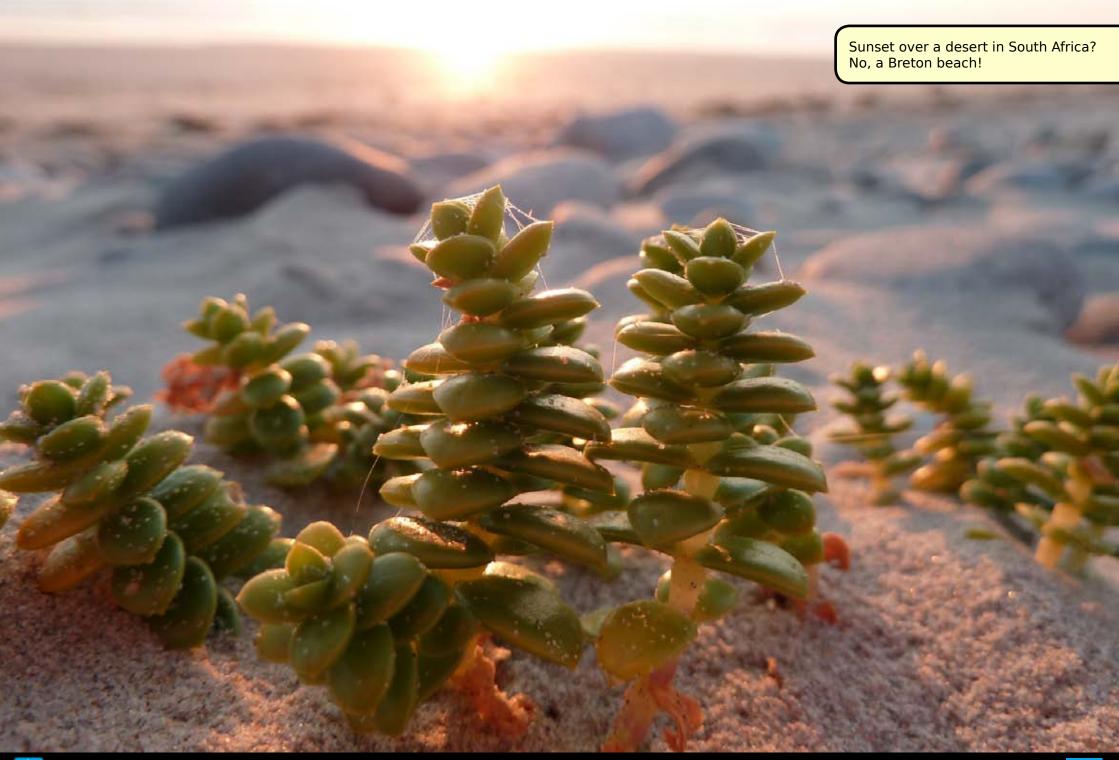


Strength and fragility

Honckenya peploides is therefore a highly specialized plant capable of colonizing an inhospitable environment where competing vegetation is rare: the upper beach. The result of this specialization is that this is the dominant plant in many places, but the downside is a very narrow ecological latitude: it cannot live elsewhere and does not support any change in its environment. It is thus a plant that is at the same time both abundant and fragile, able to appear and multiply as quickly as it can disappear.







Description

Plant: herbaceous perennial with long horizontal rhizomatous branched stems forming a wide network (in condition of regular covering by sand) or growing in dense tufts (in more stable condition). The underground stems root at each node and produce regularly spaced vertical leafy aerial stems forming a more or less loose mat. Branching is mostly underground or at ground level; aerial stems produce only a few (or none at all) vegetative branches but only short lateral branches ended with a flower (cymose flowering) only on the spring growing stems.

Leaves: glabrous, light bright green, heart-shaped to narrow lanceolate, with cartilaginous margins, sessile, very regularly opposite-decussate; the thick leaves and the very short internodes make the stem invisible or just partly visible except at the base of the stems. The leaf size slightly decreases upwards to give the stems a pyramidal shape.

Flowers: either hermaphrodite or male or female on different individuals (subdioecy)⁽¹⁴⁾. Flowers appear at the apex and at the axils of the upper leaves, either directly at the axil or at the end of a short lateral branch. Small pentamerous flower with superior gynoecium, with spatulate, rarely bifid, whitish, slightly translucent petals; petals of female flowers are often more or less undeveloped; obvious nectarian cycle of orange glands. Globose ovary with 3-4 (-5) divergent styles, highly developed in female flowers, very short or completely atrophied in males flowers and rather short in hermaphrodite flowers.

Fruit: rather big compared to the plant size; yellowish-green spherical capsule, dry when ripen and opening by three valves releasing large brown seeds.

Variability: variability concerns various characters, both morphological and physiological. Thus, this subdioecy often considered as evident, actually varies depending on the area concerned (it is weakly pronounced in western France, for example, where the individuals with purely female flowers are exceptional) but this subdioecy, not obvious anatomically, is often much more obvious on the physiological level: in many populations without anatomical dioecy, it can be noted that only some individuals bear fruits. The leaf morphology is also rather variable depending on the populations, but the comparison between populations has value only at the same growth stage because the foliage of the spring flowering stems (more spaced and more apiculate wider leaves) often differs quite significantly from that of summer vegetative stems (less wide and less apiculate leaves but thicker and less spaced) on a single individual.



This subdioecy is accompanied by a few physiological differences between males and females, which could have ecological consequences, but between the purely experimental studies and the reality in the field, the correlation is not obvious... See: Sánchez-Vilas J. & Retuerto R. (2009), in Plant Biology 11(2): 243-254.

Capricious flowering...

The flowering of Honckenya peploides starts very early, the new shoots emerge from the ground shortly after the vernal equinox and begin to flower soon after, at the beginning of April. Then flowering continues for a long time until the end of July or even until August in some places, with a peak in May-June; but flowering and therefore fruiting afterwards, are of rather variable abundance depending on the year. This variation depending on the year is of obscure origin; it may be related to environmental factors blocking the floral induction without any other consequence for the plant, since years with little flowering are not accompanied by observable vegetative disorders. Some years, mass abortions of flower buds can be observed for no apparent reason.

The factors involved in this variability in the abundance of flowering of Honckenya peploides are not clear and we don't know whether this phenomenon is observable in all areas where the plant grows. Some possible explanations for this phenomenon: low light during the stem appearing in spring, very hot spring weather, early destruction of flower stems by late storms and then regrowth of strictly vegetative stems... But it is possible and even likely that the cause of this phenomenon is multifactorial.

But be careful not to confuse this variable abundance of flowering with the constant natural phenomenon of this plant flowering near ground level: the first flower stems, very short, are gradually buried under the sand during the summer, then the second order stems, strictly vegetative, emerge and, observed at the heart of summer, the plant can give the false impression that it has not flowered.



Possible confusion

Out of flowering, it may be possible to confuse *Honckenyapeploides* with *Glaux maritima* L. (*Primulaceae*), but the latter has alternate leaves (not opposite as in *Honckenya*) and not at all or barely succulent.

The risk of confusion is quite unlikely in the middle and southern part of the area of Honckenya peploides because there, Glaux maritima inhabits the wet meadows of the upper part of salt marches (very exceptionally in rocky habitat) and so these two plants almost never coexist. However, the risk of confusion is very real in the northern part of the area of Honckenya peploides, in which Glaux maritima is much more abundant, grows in dense mats and usually colonizes the rear limit of the upper stony beaches, thus being in direct contact with Honckenya peploides. The flowering of Glaux maritima is of course very different from that of Honckenya peploides but as its flowers are very small and inconspicuous, then by far or out of flowering time confusion is possible. In addition, in an exposed position Glaux maritima tends to modify its phyllotaxis which, although remaining alternate, becomes much decussate⁽¹⁵⁾, as in *Honckenya*, with shorter internodes, making the confusion even easier. Seen close up, leaves of Glaux maritima are very different: much less thick and with multiple depressed dots on their upper surface.

It should be noted that observed *ex situ* or in pictures, non-flowering stems of *Honckenya peploides* are very similar to some South African *Crassula*!



Decussate phyllotaxis of *Honckenya peploides* is probably an adaptation to intense solar irradiation (each leaf shadowing the underlying leaf); the modification of phyllotaxis of *Glaux maritima* in this way when it grows under the same conditions it seems to be further proof of that.



Distribution

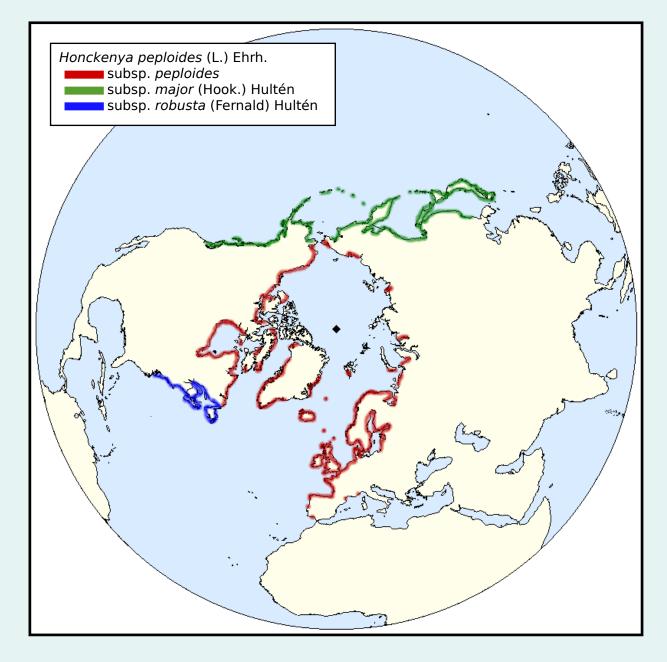
As many coastal plants, *Honckenya peploides* has a large distribution area (but reduced to a thin, dotted strip a few metres wide).

Honckenya peploides is a species of the temperate and arctic regions of the northern hemisphere; its distribution is circumboreal: it is found as well in the North Atlantic area, the North Pacific area, and in Southeast Asia.

In Europe, *Honckenya peploides* is present over the entire Atlantic coast from Portugal to the Arctic regions, including the British Isles, Iceland, the Baltic coasts and Svalbard (Spitsbergen). It is common in Arctic areas but becomes scarcer and then finally disappears as one heads southwards approaching the Mediterranean and subtropical areas. It does not like getting hot!

In the Mediterranean, *Honckenya peploides* if not totally absent is at least very rare; it was once reported in a few pin-point locations in the south of France, but it seems that it has now disappeared from them (with reservation because we have no recent data).

While still very common in many parts of its area, *Honckenya peploides* is nevertheless undergoing rapid depletion in all areas affected by urbanization and tourism and has become scarce in some places where it once abounded, due to trampling and the stupid and harmful habit of "cleaning" beaches. "Cleaning" meaning in this case killing everything that lives there and contributes to the balance of these beaches.



Map from Hultén E. (1971), The circumpolar plants, 2 - Dicotyledones.



Uses Honckenya peploides is an edible plant, raw or cooked, hence its French popular name of "Pourpier de mer" (sea purslane) which refers to both the vegetative aspect and its culinary use. It should be noted that, among those who have tasted this plant, of which we are unfortunately a part, opinions are generally unanimous in saying that to eat this plant one needs to be really very hungry... It has a less salty taste than most of the edible halophytes, it is even quite bland compared to these, but it leaves an unpleasant aftertaste in your mouth. Like many plants, Honckenya peploides is at its culinary optimum, or rather its least distasteful in the late spring or early summer, just before full bloom. It seems that in Iceland it used to be, and still is sometimes fermented into a sort of sauerkraut. If one day an Icelander invites you to his table, we advise you to prepare an excuse in advance... Young spring shoots, shortly after emerging from the substrate.

Protection

In **France**, *Honckenya peploides* is integrally protected in the region of Aquitaine (Arrêté du 8 mars 2002).





A bit of nomenclature...

Honckenya peploides (L.) Ehrh., in Neues Mag. Aerzte 5(3): 2067 (1783)

Family: Caryophyllaceae (syn. Dianthaceae).

Type: (Lectotypus) leg. anonym., s.n., sine loco, LINN 485-1 / design. Jonsell & Jarvis, in *Nordic J. Bot*. 14: 156 (1994)

Synonymy:

- ≡ [basionym] Arenaria peploides L., Sp. Pl. 1: 423 (1753)
- *Adenarium peploides* (L.) Raf.
- *Alsine peploides* (L.) Crantz
- *Ammodenia peploides* (L.) Rupr.
- \equiv Ammonalia peploides (L.) Desv.
- *≡ Halianthus peploides* (L.) Fr.
- *Minuartia peploides* (L.) Hiern
- = Holosteum succulentum L., Sp. Pl. 1:88 (1753)
- = Adenarium maritimum Raf. New Fl. 1: 62 (1836)
 - *Ammodenia maritima* (Raf.) E.P.Bicknell
 - *≡ Honckenya maritima* (Raf.) Raf.

The generic name *Honckenya* is dedicated to G.A. Honckeny, a botanist of the 18th century. This name is subject to many mistakes; one can read here and there *Honckenia*, *Honkenya*, *Honkenia*, *Honckenja*, *Honckeneja*... only *Honckenya* is correct.

The species name *peploides* is of more uncertain etymology. It must likely be understood as meaning, in Linné's mind, "looking like Peplis", *Peplis portula* L. being a fresh marsh plant.

Chromosome number: $2n = 68^{(16)}$ which is a high number, indicating a probable ancestral polyploidy.

STRANDARVE, HONCKENYA PEPLOIDES

¹⁶ H. Malling (1957), in *Hereditas* 43(3-4): 517-524.

Common names

- (GB) Sea sandwort, Beach sandwort, Sea pimpernel.
- (FR) Pourpier de mer, Pourpier des plages.
- (IT) [none]



Infraspecific taxa

Due to the very wide distribution of this species along the coasts of the northern hemisphere, one can recognize some geographic variations which have in the past been individualized to the infraspecific or even specific level. In fact, one may wonder about the reality of the individualization of these geographic variants, considering the variability of this plant in one single geographical area ...



The following presentation is only a report of raw data because we express no opinion on the merits of the inclusion of these subspecies, not knowing enough (if at all...) the distribution areas of some of these subspecies, and thus the actual differentiation *in situ* of these plants.

• Honckenya peploides subsp. peploides

The type subspecies corresponds to the populations of European and Icelandic coasts, and likely of all the arctic areas.

The subspecies or variety *diffusa*, described from the arctic regions, seems to be considered as a synonym and also, but with less certainty, the variety *latifolia*.

Synonymy:

- = Arenaria peploides var. diffusa Hornem., Fors. Oecon. Plantel., ed. 3, 1: 501 (1821)
 - *Ammodenia peploides* var. *diffusa* (Hornem.) Porsild
 - *Arenaria diffusa* (Hornem.) Wormsk.
 - \equiv Halianthus peploides var. diffusus (Hornem.) Lange
 - *≡ Honckenya peploides* var. *diffusa* (Hornem.) Ostenf.
 - *Honckenya peploides* subsp. *diffusa* (Hornem.) Hultén
 - *Honckenya diffusa* (Hornem.) Á.Löve
 - *Minuartia peploides* var. *diffusa* (Hornem.) Mattf.
- = ? Honckenya peploides var. latifolia Fenzl ex Ledeb, Fl. Ross. 1: 358 (1842)
 - *Minuartia peploides* subsp. *latifolia* (Fenzl ex Ledeb) Mattf.



• *Honckenya peploides* subsp. *major* (Hook.) Hultén, *Fl. Aleutian Isl.* : 171 (1937)

Type: leg. A.C.Waghorne, s.n., 1898; Canada, Newfoundland, Wild Cove.

This subspecies includes the populations of the coasts of the North Pacific and South-East Asia and differs mainly by its slightly longer leaves and more elongated internodes than the type.

Synonymy:

- ≡ [basionym] *Arenaria peploides* var. *major* Hook., in *Fl. Bor.-Amer.* 1(3): 102 (1831)
- *Ammodenia major* (Hook.) A.Heller
- *Ammodenia peplo*ides susbsp. *major* (Hook.) Piper
- *Arenaria peploides* subsp. *major* (Hook.) Calder & Roy L.Taylor
- *Honckenya peploides* var. *major* (Hook.) Abrams
- *Minuartia peploides* subsp. *major* (Hook.) Mattf.
- = Honckenya oblongifolia Torr. & A.Gray, Fl. N. Amer. 1: 176 (1838)
 - *Ammodenia oblongifolia* (Torr. & A.Gray) A.Heller
 - *Arenaria peploides* var. *oblongifolia* (Torr. & A.Gray) S.Watson
 - *≡ Honckenya peploides* var. *oblongifolia* (Torr. & A.Gray) Fenzl ex Ledeb.
- = Arenaria peploides var. maxima Fernald, in Rhodora 11: 113 (1909)
 - *Ammodenia maxima* (Fernald) A.Heller
 - *Ammodenia oblongifolia* var. *maxima* (Fernald) Nakai
- = Arenaria sitchensis D.Dietr., Syn. Pl. 2: 1565 (1840)
- *Honckenya peploides* subsp. *robusta* (Fernald) Hultén, *Fl. Aleutian Isl.* : 173 (1937)

Typus non designatus?

This subspecies includes the populations of the Atlantic coast of North America and differs mainly by its aerial stems being a little more prostrate and creeping than in the type and very strong succulence.

Synonymy:

- ≡ [basionyme] *Arenaria peploides* var. *robusta* Fernald, in *Rhodora* 11: 114 (1909)
- \equiv Honckenya peploides var. robusta (Fernald) House
- *Minuartia peploides* subsp. *robusta* (Fernald) Mattf.



Cultivation notes

From a horticultural point of view, *Honckenya peploides* is more interesting for its beautiful and very tidy, shiny foliage than for its rather dull and inconspicuous flowers. But the interest of the beautiful glossy foliage is nothing compared to the interest of its ecology. Bend your ear to this plant and you'll hear the sound of the wind and waves! In welcoming it in your home, this is not just a simple succulent that you'll host but a beach in miniature with its ever so distinctive ecosystem. To succeed in its culture, you'll have also to always keep in mind the particularities of this ecosystem. (cf. supra).

Propagation

The multiplication of *Honckenya peploides* can be done by seed, which is reputedly easy, but it's much simpler and easier to propagate it from cuttings; its stems (leafed stems or rhizomes) rooting spontaneously at nodes is also the way it propagates in the wild. Vegetative propagation also has the advantage of allowing a choice of the sex⁽¹⁷⁾ of the plant in cultivation (male, female or hermaphrodite).

Some tips for effective care of cuttings of this plant: don't hesitate to bury the cuttings horizontally in moist sand while leaving nothing more than the top out of the sand. Don't wait until the cuttings are rooted to moisten the sand, as you would do with a usual succulent, but moisten regularly and allow to dry briefly between watering. You can also alternate watering with fresh water and sea water (one out of three, for example). By doing so, you will only replicate the way the torn fragments of this plant root in nature.

The difficulty to multiply this plant is not technical but logistical: getting seeds or cuttings is not easy when you live a long way from the sea...

One study (Sánchez-Vilas J. & Retuerto R., l.c.) demonstrated a greater succulence in female individuals, but it is based on tissue analysis and, in practice, the difference in succulence between genders is not obvious...





Keeping it in cultivation

It's one thing to propagate a plant and another thing to cultivate it. We confess to having little personal experience of the cultivation of *Honckenya peploides*, because we have the opportunity to easily observe this plant in its natural environment; but since some do cultivate it (botanical gardens, research culture), the challenge should not be insurmountable, despite its very particular ecology. As we have already mentioned, it is its ecology as well as its beauty that make this plant so attractive and incites one to take on the challenge of its cultivation.

One thing is sure: *Honckenya peploides* must be grown outdoors in full sun, however this plant does not like high temperatures; don't forget that it has northern affinities. Kept in a greenhouse in summer, it turns yellow in a few days and quickly dies. Even outside, it fears too intense or prolonged heat (its behavior *in situ* depending on the latitude shows that, cf. supra). It is probably unrealistic to expect to keep it a long time in life elsewhere than in the oceanic and continental regions with cool summers i.e. the more northern continental regions.

For potted cultivation, a wide and shallow pot is probably better because of the long rhizomatous nature of the plant, this rhizomatous behaviour being variable according to the depth buried: if the plant is regularly buried under the substrate it will grow in a creeping rhizomatous way, otherwise it will adopt a more caespitose aspect.

As a substrate, in the absence of coarse sand sea, a little limy sand, not too fine, mixed with fresh little decomposed compost, will certainly do the job. Do not be afraid to have a "heavy hand" with the fertilizer, not only to feed this greedy plant, but also to maintain the high osmolarity of the substrate which is appreciated, at least temporarily, by all the maritime plants. Alternating heavy fertilizer supplies with abundant washing of the substrate with pure water will reproduce fairly well its conditions of life *in situ*.

A pinch of salt occasionally will certainly not displease it, or some watering with a little sea water (natural or reconstituted, see the aquarium stores) if available. Moderate but regular supplies of salt (NaCl) will have the effect of increasing the succulence of the plant as in most maritime succulents.

You can also try to cultivate *Honckenya peploides* in the open ground, in light soil, because winter moisture is not a problem for this plant.

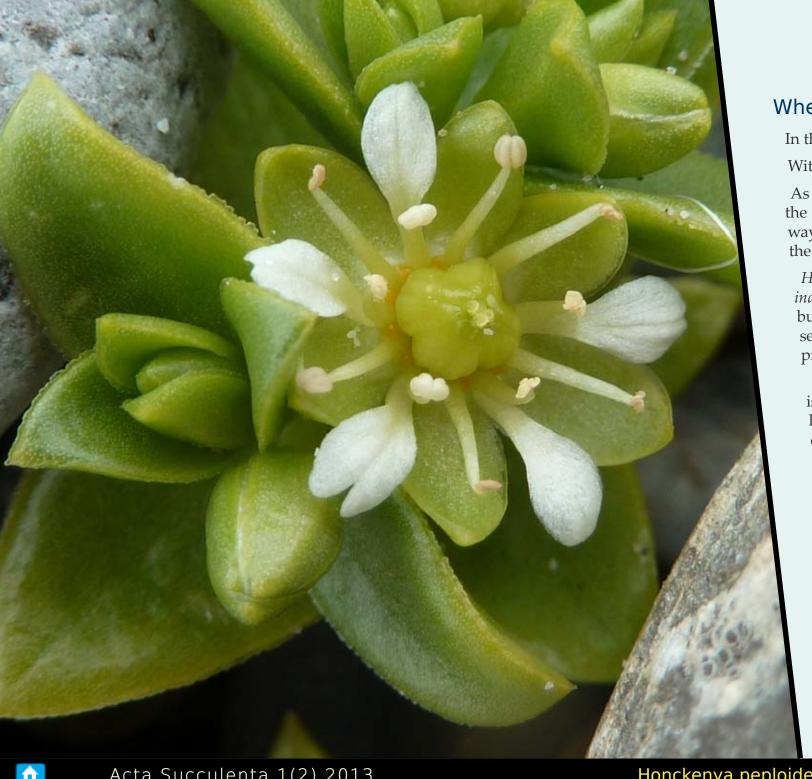


Hardiness

It's difficult to appreciate how *Honckenya peploides* really withstands frost. The fact that it grows naturally in Alaska, Greenland, Lapland, Spitzbergen and at some points of the Siberian coast, and that these places are not especially known for their mild winter climate, should not create an illusion: in these regions this plant grows very close to the water and thus has a much warmer microclimate than a few meters further back. In addition, it winters buried in the substrate which is heated by the sea water, which is much hotter than the ambient air. Its real resistance to low temperatures should not hence be overstated because of its presence on the edge of the Arctic areas.

Honckenya peploides is certainly not a very frost-sensitive plant and a few degrees below zero doesn't frighten it, but perhaps not much below. Moreover there is surely some hardiness variation depending on the geographical origin of plants because between the Portuguese coast and these of Spitsbergen, there is still some difference, even at the water's edge!





Where to get this plant?

In the trade? It is almost unknown!

With amateurs? Almost none cultivate it!

As it is not easier to get seeds than to get the plant itself, there remains only two ways: botanical gardens or collecting in the wild.

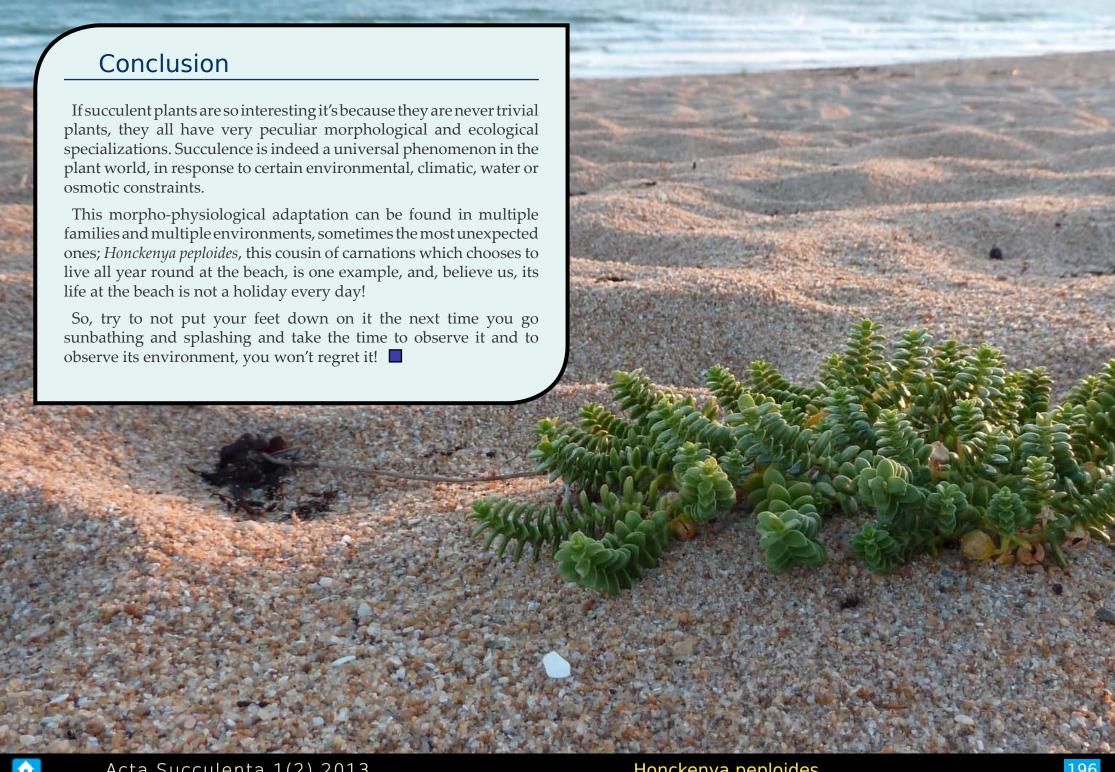
Honckenya peploides is present in the index seminum of some botanical gardens, but it is rare that they would agree to sell seeds to individuals; they normally only practice exchange between institutions.

The only remaining way therefore is harvesting in the wild. If you don't have the opportunity to go to the coasts that host this plant, you can always find a friend or a neighbour who will go there on holidays and who could bring you back a fragment of it; even if he knows nothing about plants, a photo will be enough for him to recognize it easily without risk of error. That is possible only outside of the areas where the plant is fully protected, of course.

Have no compunction to collect or make a cutting. We reported above that this plant is in regression at many of its locations, so it seems illogical and irresponsible to promote collecting it; but we also noted that this decline was the result of trampling and human practices of beach "management" and in no way the result of collecting. What's the removal of one or two stems compared to the damages from storms that this plant faces regularly? Nothing, strictly nothing! Honckenya peploides is perfectly adapted for a quick recovery of its vegetative system if destroyed, so one stem more or less, what's the problem? None! No stupid fundamentalism! The true protection of nature is not that. Do not hesitate to pick up a piece if you want to try its cultivation! If you want to really protect it, you should try to protect its natural environment, but the plant itself does not need you, it will manage very well alone.

The natural area of *Honckenya peploides* being huge, its geographical origin is certainly not without importance in the greater or lesser difficulty of its cultivation. Thus, Arctic plants have a reputation for being difficult to keep alive outside their native shores.









TN the large group of the epiphytic cacti, Schlumbergera ×buckleyi is an old garden hybrid, created in the mid-Inineteenth century, by crossing Schlumbergera russelliana (Hook.) Britton & Rose and Schlumbergera truncata (Haw.) Moran. This hybrid plant seems totally unknown in the wild.

Schlumbergera ×*buckleyi* is especially famous as the "Christmas" Cactus" of our grandmothers and is one of the main plants in the traditional assortment of indoor plants as well as being one of the most indestructible. Many people also know it only under that name.

Schlumbergera ×buckleyi is also a plant that forces one to consider a new perspective on the concept of the cultivated plant and on the interpretation of human-plant relationships.

Ecology

The ecological requirements of Schlumbergera ×buckleyi are derived directly from those of its wild relatives. These are epiphytic plants of the rainforest, more exactly from the forests of the coastal ranges of southern Brazil. Although these are Cactaceae, their ecological needs have nothing to do with those of terrestrial Cactaceae from dry tropics; these needs are rather similar to those of some orchids with which they cohabit in situ.

The preferences of these plants are as follows: damp heat and bright light without direct sun, and an aerated humus substrate.

Highly evolved Cactaceae

The succulence of *Schlumbergera*, as in most other epiphytic cacti, is moderate and their drought tolerance is very limited; just enough to withstand a temporary, non-regular, drought, but no more. It should be understood that the succulence of these epiphytic *Cactaceae* from the rainforest *is not an adaptive character but an ancestral character*, an old genetic memory of the xerophytic *Cactaceae* from which they were derived⁽¹⁾. These epiphytic cacti therefore represent a highly evolved stage compared to xerophytic terrestrial cacti. Let's point out that there is no scale of values in the concept of evolution and an evolved plant is not a plant more efficient environmentally than a less evolved cousin and sometimes less, because overadaptation to an environment increases vulnerability to any changes in this environment.

The succulence of these forest cacti is no longer very useful for them because their stems can always accumulate a little water but their roots have become very sensitive to drought and die quickly if it continues, thus preventing the plant in rehydrating properly. These epiphytic ca

rehydrating properly. These epiphytic cacti are still succulent morphologically but are no longer true xerophytes.

They oung shoots of *S.* × *buckleyi* remembering that their ancestors were columnar cacti.

The "memory" of this ancestry is obvious in many species at the seedling stages, when they are very similar in appearance to those of columnar cacti. This is sometimes also seen in cases of physiological rejuvenation of some stems after severe pruning as well as in significant etiolating: in this case there is a change of the appearance of stems which take on a much more cereiform appearance (cylindrical section, increase in the number of ribs and the appearance of fine spines).



From horticulture to "domicolism"

Schlumbergera ×buckleyi has been common for so long as a "houseplant" and that in the sense of being completely independent of horticultural production and trade channels (this criterion is important) that we can speak about a naturalized anthropochorous⁽²⁾ plant, the biotope of which is constituted by the human habitats.

This is definitely not a joke or an illusion, it's simply to point out some human practices among the factors of natural selection and thus, to broaden the often too narrow concept of the "natural".

Yes, a human habitat is a biotope like any other biotope, with its biocenosis⁽³⁾; it would be ridiculous to deny that, and Schlumbergera *buckleyi is a common component of this biocenosis. This plant performs its entire life cycle in this type of biotope: it multiplies (vegetatively) there, it lives and dies there and its anthropochorous dispersion occurs only from and to similar biotopes.

The human-plant relationship in this case is a mutualism comparable to many other types of mutualism between plants and animals; we can thus talk about ectosymbiosis⁽⁴⁾. The case of *Schlumbergera* ×*buckleyi* therefore has nothing to do with the majority of houseplants that are most often no more than foreigners unable to survive in the long-term in this type of biotope without a regular reinforcement of their strengths by external inputs of horticultural origin.

The ecological concept of "domicolous" (5) plants, which could be developed more fully, therefore applies perfectly to this plant, as well as some other plants of the traditional assortment of indoor plants.



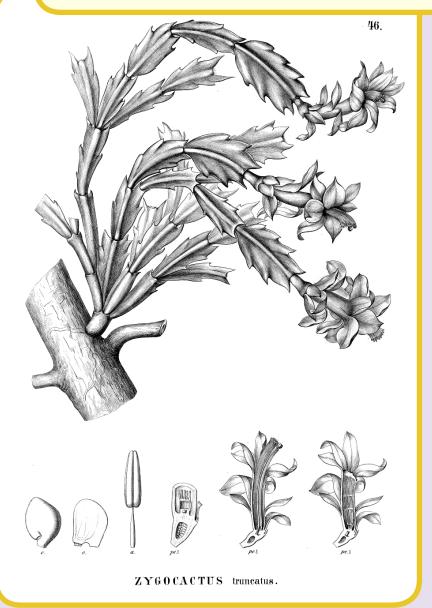
An anthropochorous plant is a plant whose dissemination (seeds, cuttings, any kind of propagules) is done by Man, voluntarily or involuntarily. Similarly, one speaks of zoochorous plants when the dissemination is done by animals in general, anemomochorous plants if by the wind, thalassochorous plants if the sea is the vector, etc., and barochorous plants when the only vector of dissemination is gravity.

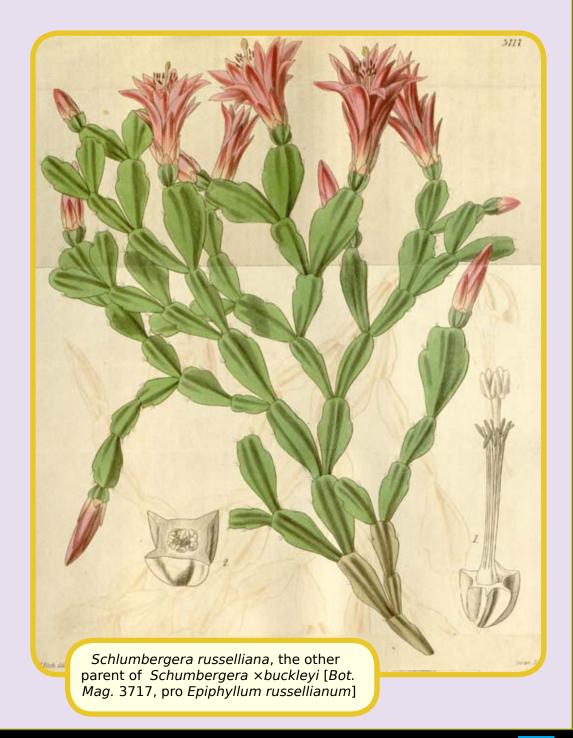
A biotope is a space frame with all the parameters associated to it. A biocenosis is the set of living organisms which populate a biotope and interact with it. The set biotope + biocenosis + interactions is an

A symbiotic relationship involves a mutual benefit for partner organisms: the benefit to the plant is evident here (food, water, multiplication, etc.), for Man it's less material, it's within the realms of enjoyment (evocative power of the plant, satisfaction given by the response to cultivation, etc.).

From the Latin "domus" house or home, and "cola" inhabitant. It's a neologism, the name is of little importance, only the concept referred to by this name is important.

Schlumbergera truncata, one of the parents of Schumbergera ×buckleyi. The artist has obviously worked from a remote branch and confusing epiphytism and parasitism, he has imagined a freakish base, like a mistletoe! [Martius, Flora Brasiliensis, pro Zygocactus truncatus]





Description

Schlumbergera × buckleyi has kepta vegetative aspect very close or even identical to that of one of its parents, Schlumbergera russelliana. However its flowers are intermediate in appearance between the flowers of S. russelliana and those of S. truncata, its other parent.

Plant: perennial, flared and multibranched from the base, pendent (deflexed stems).

Stem: articulated in string of short separate segments; each segment is a flattened branch with two lateral ribs and a protruding central vascular axis, morphologically and functionally mimicking a leaf (phylloclade), with some discrete areoles along the margins and a linear apical largest areole, where flowers and new articles appear. Sections of the older segments gradually become round and woody and they merge into a rounded stem with slightly peeling fine bark.

Flower: terminal, continuing along the axis of the segment; epigynous, tubular corolla slightly zygomorphic with many slightly recurved petals arranged in superimposed levels.

Fruit: pyriform, glabrous and smooth berry; translucent pink when ripe. The fruit is rarely observed (the self-sterile plant multiplies vegetatively), its appearance is usually the result of cross-fertilization with other species in nearby cultivation (most often *S. truncata*).



Possible confusion

Confusing *Schlumbergera* × *buckleyi* is difficult except with one of its parents: *Schlumbergera russelliana* or *Schlumbergera truncata*.

The possibility of confusion with *Schlumbergera russelliana* is mainly theoretical because this plant is very rare in cultivation, except in specialized collections. The confusion is nevertheless easily made because the vegetative aspect is similar, but the flowers of *S. russelliana* are a little smaller, perfectly radially symmetric and bear non-recurved petals. In addition, it is less vigorous and less floriferous in culture than *S. ×buckleyi*. From a strictly horticultural point of view, *S. russelliana* therefore has no interest compared to its hybrid *S. ×buckleyi*, from which it differs little, and only a few enthusiasts cultivate it, as a curiosity or a botanical necessity in order to complete their collections.





On the other hand, confusing *Schlumbergera* ×buckleyi with *Schlumbergera truncata* is a very real possibility, mainly with the many cultivars of the latter, and this confusion is often made. Indeed, the cultivars of *S. truncata* invade garden-centres every fall and are widely used as houseplants. The distinction is nevertheless easy: *Schlumbergera* ×buckleyi has much less zygomorphic flowers than those of *S. truncata*, and they continue along the axis of the stems (they are clearly skewed upwards in *S. truncata*, forming a distinct angle with the stem that bears them), its petals are less strongly recurved, its segments are smaller and toothless, the old stems become rounder and woodier and the plant can get to a much larger size over time than that of *S. truncata*. *Schlumbergera* ×buckleyi also flowers one month later, which fully justifies its name "Christmas Cactus", which is slighltly misused in the case of *Schlumbergera truncata*.

A final difference between *Schlumbergera* × *buckleyi* and its parents, one that is not immediately visible but is quickly noted: it is incomparably sturdier and more long-lived in cultivation!



Lastly *Hatiora rosea* (Lagerh.) Barthlott (syn. *Rhipsalis rosea* Lagerh.) deserves a mention. It looks like a tiny version of the previous and flowers like it in the spring. Out of flowering its segments can evoke those of *Schlumbergera* × *buckleyi* but they are much narrower and less flat and their apex is often brownish. Much rarer than the previous in cultivation, it is nevertheless offered for sale from time to time in the garden-centres as a houseplant.

Further confusion could possibly occur in the vegetative state with cultivars and hybrids of *Epiphyllum gaertneri* (Regel) W.Watson (syn. *Hatiora gaertneri* (Regel) Barthlott), which is also common in garden-centres. But this is the "Easter Cactus" and, as its name suggests, it's necessary to have lost your calendar in order to confuse it with the "Christmas Cactus"! In addition to a very different flowering time, their flowers are not alike; those of *E. gaertneri* are radially symmetrical, without a tube and with non-recurved petals. The segments of *E. gaertneri* have a shape similar to those of *Schlumbergera* *buckleyi* but they are much larger and their apical areoles bears many setiform prickles; however the overall size of the plant is smaller.



Cultivation notes

Nice and easy as it is to grow, this hybrid is an undeniable horticultural success.

Schlumbergera ×buckleyi is happy almost everywhere, resists almost everything and lives for a long time. Fifty years and older individuals are extremely common and century-old individuals are not exceptional. It's an indestructible plant which you receive from your grandmother and which you are sure, with a little care, to be able to bequeath to your grandchildren!

This remarkable strength and durability means this plant is almost absent from the trade because it's not profitable enough!

Where to cultivate it?

Surely not in a cactus glasshouse, where it is much too hot and dry.

Schlumbergera ×buckleyi likes moderate heat and humidity or at least not too dry. It will be thus very happy in the house near an east or west-facing or even north-facing window, but absolutely never in a south-facing one. The plant will love being placed it outside in a shaded place in summer and nothing will make it happier than a good rain shower from time to time (but watch out for snails that love it as much as you!) but it can spend its entire life (which will be much longer than yours) in the same place in the house.

Some fans of epiphytic cacti grow *Schlumbergera* ×*buckleyi* with other epiphytic cacti in dedicated greenhouses (moist and shaded) but, in my opinion, it loses much of its charm in such a situation. Indeed, Schlumbergera ×buckleyi is, under a temperate climate, a traditional old houseplant and it is much more pleasant and evocative to cultivate it in the house as our grandmothers, and their grandmothers before them, have always done.



Containers and contents

Schlumbergera ×*buckleyi* belongs to the epiphytic group of cacti and therefore grows in a light, aerated, and rather acid humus substrate.

Its roots form a rather small and compact ball and hence it will behave better in a relatively small pot, but without excess because this plant can grow very large with age, so the size of the pot should increase with it but always remaining slightly disproportionate relative to its size. It should always give the impression that it's growing in a too small pot size and it can stay for many years in the same pot. It's the slowdown in growth and not the "look" that will tell you that repotting into a larger pot is needed.

Watering

Schlumbergera ×buckleyi enjoys regular but moderate watering.

If the root ball is dry for too long, the plant withers and its roots can die; the plant will then take a long time to recover. In such case, removing the dead roots then letling the plant root in new substrate is often faster than waiting for it to make new roots in the old substrate.

Conversely, if the root ball remains constantly saturated with water, the roots may rot; the plant will make new ones but again, this will take time and treating the stock or the big stems as cuttings is faster.

The best regimen for watering is to keep the root ball permanently and slightly moist, but never soggy, leaving it drying from time to time but never for more than 2-3 days. Do not panic, the plant has strong constitution and will therefore withstand most watering errors.



Propagation

Making cuttings of *Schlumbergera* ×*buckleyi* is easy, using stems with 3-4 segments, rooting is very fast because segments bases usually already have some aerial rootlets. The individual segments are also usable but getting a presentable plant takes a little longer. As noted above, making cuttings with large woody stems is quite possible, but it is important to let them dry and wounds heal before planting.

IMPORTANT: cuttings will root much more easily if they are *torn off* and not cut. Indeed, if the cut removes the narrow base of the segment, it will not root or will only with great difficulty. You can put the cuttings directly into the substrate or into a glass of water if you want to make many cuttings to distribute them, for example.

Seed raising is also possible because this hybrid plant is fertile, as well as male as female parents⁽⁶⁾. This plant being a hybrid will result in an inhomogeneous and not necessarily very interesting offspring. In addition, seed-production is a very theoretical possibility because the plant is self-sterile and finding two different clones is not easy... There remains the solution of backcrossing with one of its parents,

An old engraving of a plant grafted on a stem, a method

which, however, given the morphological proximity of these two plants is of little interest.

Grafting is sometimes used, especially by grafting on a rootstock forming a high trunk to highlight the weeping aspect of the plant. That was widely practiced once but is now out of fashion.



of propagation and cultivation

which was once very popular.

T.H.Boyle & al. (1995), Pollen Germination, Pollen Tube Growth, Fruit Set, and Seed Development in Schlumbergera truncata and S. ×buckleyi, in *J. Amer. Soc. Hort. Sci.* 120(2): 313-317.

My Christmas Cactus almost never blooms!

Many enthusiasts complain about the non abundant or insignificant flowering of their Christmas Cactus, while at the same time it is very healthy and growing well.

The reason is always the same: an excess of light during the fall!

For maximum flowering, the temperature is unimportant, but in the fall it is imperative to keep the plant in a dark room without artificial light at night or in the morning, even briefly, so it has short days which will induce flowering. Caution, the light does not need to be intense to inhibit flowering of *Schlumbergera* ×*buckleyi*: just a pilot light will have the same effect as a spotlight focused on it.

This fact is generally known by those who grow this plant but it is sometimes misunderstood. The mistake is to confuse darkness and night. For this plant, twilight and daylight are the same! Indeed, the sensitivity of plants to the presence of light (and therefore to the day length) should not be confused with their need for light intensity for growth and photosynthesis. A plant detects the presence of light by its phytochromes, which are molecules that have an extreme sensitivity to light compared with chlorophyll. A plant can thus vegetate and etiolate because it stands in too shady a place while considering itself as much too enlightened to bloom! Indeed, it's the criterion of *intensity* that determines photosynthesis and good growth of the plant, but it's the criterion of *duration*, alone, that determines the induction of flowering.

In order to enjoy the generous flowering of *Schlumbergera* ×*buckleyi* to the maximum, it is likely that you will want to move it into an inhabited room, namely a room lit up in the evening. Don't do it too early because this will lead to the downfall of most young buds. Instead, wait until the first flowers open before moving the plant, any bud loss will be much lower.



Where and how to get the plant?

Paradoxically, *Schlumbergera* ×*buckleyi* is, for a long time, a very common plant in cultivation and yet is nevertheless very difficult to get in the trade.

The reason is simple: this plant is virtually unsaleable... In fact, most people already have it, it is indestructible, it easily survives its owners and it is multiplied by cuttings without difficulty. The maintenance and dissemination of this plant is therefore outside the commercial circuits. The few people who don't have it and want to correct this anomaly will find easily a cutting from someone in their family or a close neighbour.

It has been like that for over a century, and that's not likely to stop.



A bit of nomenclature

Schlumbergera ×*buckleyi* (T.Moore) Tjaden, in *Nat. Cact. & Succ. Journ.* 21: 93 (1966)

It should be noted that D.R.Hunt also attributes this combination to himself: *Schlumbergera* × *buckleyi* (T.Moore) D.R.Hunt, *Synopsis of Schlumbergera*, in Kew Bulletin, 23(2): 259 (1969)

Family: Cactaceae.

Typus not designatus?

Synonymy:

(= Schlumbergera russelliana × Schlumbergera truncata)

- [basionym] *Epiphyllum ×buckleyi* T.Moore, in *Gard. Comp. Flor. Guide* : 41 (1852)
- \equiv Schlumbergera \times buckleyi 'Buckleyi'
- *≡ Schlumbergera* 'Buckleyi'
- *≡ Zygocactus* ×*buckleyi* Hort.
- *≡ Epiphyllum* ×*ruckerianum* Hort. ex Lem, in *Ill. Hort*. 8, Misc.: 5 (1861) [pro sp.]
- = Epiphyllum ×bridgesii Lem., in Ill. Hort. 8, Misc.: 5 (1861) [pro sp.]
 - *≡ Epiphyllum truncatum* var. *bridgesii* (Lem.) Rümpler
 - Schlumbergera ×bridgesii (Lem.) Loefgr. in Arch. Jard. Bot. Rio de Janeiro 2: 32 (1918)
 - = *Zygocactus* ×*bridgesii* (Lem.) Linding., in *Beih. Bot. Centralbl.* 51A: 378 (1942), in obs.
- = Epiphyllum ×rollissonii T.Moore, in Gard. Comp. Flor. Guide: 41 (1852), in adnot.
 - $\equiv Schlumbergera \times buckleyi \text{ 'Rollissonii'}$



The genus name *Schlumbergera* is a dedication to a cactus collector of the nineteenth century. The species name *buckleyi* is a dedication to the breeder who is deemed to have created this plant in the 1840s: William Buckley, from the Rollisson Nurseries in Great Britain.

Quarrel over names...

The correct name to apply to this hybrid is not consensual. Indeed, its first name is *Epiphyllum buckleyi* T.Moore (1852), *Epiphyllum bridgesii* Lem. (1861) is later BUT its recombination under *Schlumbergera* is earlier (1918) than that of *E. buckleyi* (1966).

Which is the correct name to be used for this plant? The answer to this question is not unique, because it varies depending on the answers to the two following questions, which are essentially based on taxonomic opinions and not on nomenclatural facts:

- **A.** Do you consider that *Epiphyllum buckleyi* T.Moore and *Epiphyllum bridgesii* Lem. designate the same plant ? Yes: A1, No: A2.
- **B.** Do you consider that the common plant in cultivation is related to the genus *Epiphyllum* (B1) or the genus *Schlumbergera* (B2)?

Depending on the answers, the correct name of this plant will be:



A1+B1: Epiphyllum ×buckleyi T.Moore

A1+B2 : Schlumbergera ×bridgesii (Lem.) Loefgr.

A2+B1: Epiphyllum ×buckleyi T.Moore

A2+B2: Schlumbergera ×buckleyi (T.Moore) Tjaden

NB: its attachment to *Zygocactus* is illegitimate; the names involved were not validly published.

One note that *Schlumbergera* ×*buckleyi* (T.Moore) Tjaden is the name most often used in the literature, which implies that the authors using this name consider that *Epiphyllum bridgesii* Lem. is an illegitimate name, which is not the case, or that it's a different plant⁽⁷⁾ from *Epiphyllum buckleyi* T.Moore, although this is difficult to assert from reading its description and diagnosis...

The nomenclatural debate is not the primary focus of this article; for this reason this is the most common name for this plant that is used here, but without any certainty that this name is the most relevant...

D.R.Hunt (l.c.), for example, cannot be followed: he considers it as a synonym of *Schlumbergera truncata* while Lemaire explicitly describes the lateral margins of segments as "absolute edentato".

Common names

(**GB**): Christmas Cactus, Thanksgiving Cactus.

(FR): Cactus de Noël, Langue de femme.

(іт): Cactus di Natale, Lingua di suocera.

Related cultivars

According to the rules of nomenclature, the name *Schlumbergera* × *buckleyi* applies to ALL hybrids of type *Schlumbergera russelliana* × *truncata*. For greater precision in identification, the universally cultivated clone can therefore advantageously be named as a cultivar: *Schlumbergera* × *buckleyi* 'Buckleyi'.

Indeed, there are some other cultivated clones of *Schlumbergera* × *buckleyi* in cultivation. They are very close to each other and can therefore be confused with 'Buckleyi'. Some are really different clones, probably coming from the original cross(es), some others are probably the result of somatic mutations, i.e. vegetative mutations of some stems, which appeared over time and were then selected (intentionally or unintentionally) and maintained by cuttings. This selection of vegetative mutations⁽⁸⁾ is frequent in older hybrids which were vegetatively propagated.

Some examples include:

- 'Le Vesuv' deemed to have a denser habit and a slightly later flowering than 'Buckleyi' but it is most often the latter which is found under that name...
- 'White Buckleyi'
- 'Peach Buckleyi'
- 'Red Buckleyi'



Be wary, however, of some so-called colour variations because all *Schlumbergera* have the particularity of having flower colours varying according to the temperature: the lower the temperature the darker and more intense the colour. The flowers of two individuals can be compared only in uniform culture.

At last *Schlumbergera* ×*buckleyi* 'Rollissonii', probably coming from the same original cross, which has uniform magenta flowers (pinkish-white tube in 'Buckleyi'). It is much rarer in cultivation than 'Buckleyi'.

⁸ Vegetative mutations are often chimeras, i.e. a mixture of several genetically different cell lines, one of which could take over the others in time. Chimeras can be induced artificially by using colchicine or ionizing radiation. Professional breeders do that routinely to create new cultivars of *S. truncata*, but the cultivars obtained are often unstable and spontaneously regress to type plants in a few years.







ours XIV, king of France, was known as the Sun King. Nobody could say whether he knew the houseleek we are ■going to present to you now, but one might think he did, since like Louis XIV, for its characteristics this houseleek deserves this title more than any other species: the colour of the sky of its leaves, that of the sun of its flowers, the proud bearing... Yes indeed, this houseleek is an aristocrat, the king of houseleeks, the Sun Houseleek!

On the crystalline and effusive central-eastern Alps, houseleeks are common on well exposed rocky areas, but at higher altitudes, one species of a medium-large size catches the hiker's eye, for its regular aspect and its very attractive colours, amply paying back the climbing effort with its beauty.

This beautiful houseleek is Sempervivum wulfenii Hoppe ex Mertens & W.D.J.Koch, the Wulfen's houseleek, named after the Austrian Jesuit and botanist F.X. von Wulfen (1728-1805), author of Flora Norica, and the first to describe this plant as Sempervivum globiferum L., a Linnean name that at the time included all the yellow flowered species (this name is currently reserved to a single species of the Jovibarba subgenus). The attribution of the name wulfenii to Hoppe is based on the fact that he was the first to name it in such way in a letter addressed to the taxon's authors.



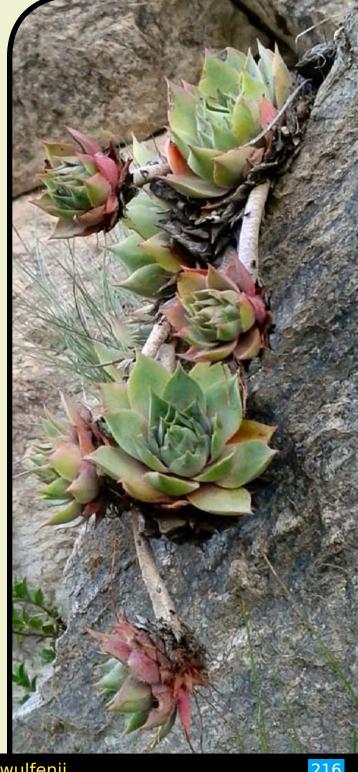
Description

Sempervivum wulfenii is generally easy to identify, both with and without flowers.

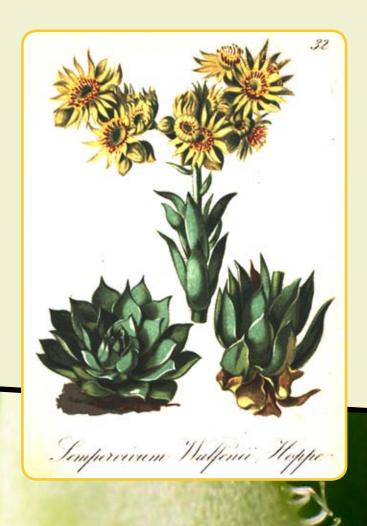
Clump: like all the houseleeks S. wulfenii forms a clump of monocarpic rosettes, expanding by lateral offsets. The clump is rather sparse: the daughter-rosettes are few and seldom completely surrounding the mother-rosette, since it normally produces only 1-3 stolons each year, and rarely more than that. The stolons are short, rarely exceeding the diameter of the mother-rosette, and are not produced during the year it flowers.

It's interesting to note that the stolons of *S. wulfenii* are particularly thick (probably the thickest of the entire genus Sempervivum) and can persist for several years, both in Nature and in cultivation. These thick and persistent stolons are glabrous, sometimes bearing true small leaves, rather than simple spaced scales. It would seem that the stolons of *S. wulfenii* are less evolved compared to the other species of the genus: from a morphological and functional point of view they are little more than basal branches, so much that the daughter-rosettes root rather slowly and don't readily detach from the connecting stolon. The stolons' aspect of *S. wulfenii* is thus one of the most primitives of the genus Sempervivum, reminding the lateral branches of the close Macaronesian genera (Aeonium, etc.), but this similarity doesn't necessarily imply any direct relationship.

Adult rosette: robust, with a few leaves, regularly arranged without showing any marked anisophylly⁽¹⁾ (contrary to *S. tectorum*, which is often very anisophyllous). During the vegetative stage, the cone formed by the central leaves is often considered a distinctive character of the species: in reality this characteristic is not constant and very variable according to the geographical origin of the clones, it can be very evident or not existent in the wild, but whenever present, the central cone is indeed very characteristic for it remarkably contrasts with the well spaced and wide external leaves.



Anisophylly: difference in shape or size between leaves closely located at the same level of the branch or stem, hence with comparable age and function. The vegetating rosettes of houseleeks frequently show anisophylly.



Leaves: the leaf blade is wide and glabrous, its margins fringed with mainly *glandular* cilia, irregular and often rather sparse. It should be noted that the mucous gland on the cilia's apex has often a reddish colour, but this can be generally appreciated only with a lens. The association of these characters (glabrous leaf blade and irregular, glandular cilia) allows to easily identify *S. wulfenii* even outside its flowering period, so that the oft-mentioned confusion with *S. tectorum*, isn't actually possible (*S. tectorum* has cartilaginous cilia, more regular and *not glandular*).

The leaf colour is a rather pronounced and nice glaucous, with a more or less pronounced basal blotch from cherry red to violet, relatively constant in good exposure. This blotch has rather indefinite borders and gradually merges with the glaucous colour of the leaf blade. There isn't a clear apical spot, but some specimen strongly exposed to sunlight can present a small and rather undefined mahogany spot, especially at the beginning of the growing season. This apical spot, if present, is always less evident than the basal one. During winter, the entire leaf attains a deep purple colour, that disappears at the beginning of the growing season in spring.

Inflorescence: on top of a rather tall and erect stalk, the inflorescence itself is rather small in comparison, generally terminating with three relatively short lateral branches. Unlike the rosette, the inflorescence is hairy.

Flower: large and markedly polymerous (often more than 12 divisions); yellow petals with unconspicuous reddish basal blotch; reddish staminal filaments contrasting with the yellow petals.

Variability and subordinate taxa

Sempervivum wulfenii Hoppe ex Mertens & W.D.J.Koch, in Röhling J.C., Deutschlands Flora, ed. 3, vol. 3: 386 (1831)

By using geographical and morphological criteria (and ecological, but at a lower scale of importance), this species can be divided in two groups, numerically very different, but nomenclaturally matching two distinct subspecies:

- Sempervivum wulfenii subsp. wulfenii
- Sempervivum wulfenii subsp. juvanii





Sempervivum wulfenii subsp. wulfenii

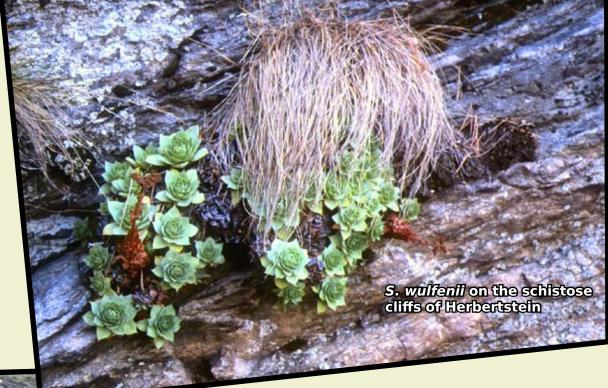
Completely glabrous plant. Type subspecies, representing all the Alpine populations and thus the vast majority of the individuals of the species, covering almost entirely its distribution range.

It's typically a high altitude plant that normally doesn't descend to medium and low elevations. Nevertheless, there are a few rare, apparently relict, small locations at low altitude at the south-eastern foot of the Alps (Mürtal, Styrian Prealps).

The subspecies *wulfenii* represents the "standard" morphotype of *S. wulfenii* and it's thus very glabrous during the vegetative stage, having only a hairy inflorescence. However, the younger rosettes sometimes show some fleeting hairs. It's also possible to see some temporary hairiness in particular cases of physiological "rejuvenating" of the adult rosettes' meristems: in practice this happens as a consequence of the destruction of the vegetative apex caused by rot or other causes of heavy traumatic or physiological stress, so that the rosette resumes growth developing obvious juvenile characters, including an ephemeral hairiness on the leaf blade.

The isolated populations of Styrian Prealps

At some low-altitude locations, in the south-east of Austria (at Riegersburg and at Herbertstein), the plants show, apart from an unusually low altitude, some transitional morphological characters into the subspecies *juvanii*, in the form of a short-lasting and thin hairiness. This difference is minimal however, and these forms are directly linked with the subsp. *wulfenii*. More than the presence of fair amount of hairiness, what differentiates them from *wulfenii stricto sensu* is its amount and persistence, and, mainly, the ease with which this hairiness is produced, whilst the appearance of even a few hairs on *S. wulfenii* subsp. *wulfenii* during the vegetative stage is rather infrequent, very limited and short-lasting.

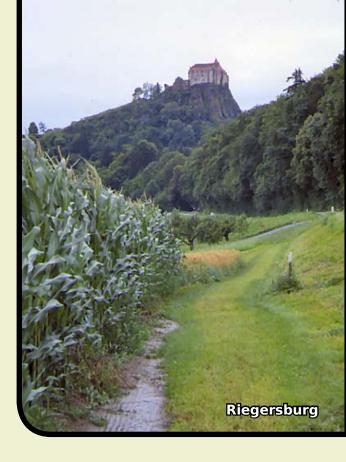




The presence of such hairiness on the Riegersburg and Herbertstein plants, albeit moderate, partial and ephemeral, has some consequences: this relative morphological differentiation compared to *S. wulfenii*-type as it's known from its high altitude locations, indicates that these ectopic populations are real natural populations, rather than simple naturalizations of once cultivated plants originating from the core of the Alps, as it's been sometimes hypothesized. In our opinion, considering these low altitude populations as spontaneous, has found a definitive confirmation.

The ability to grow at low altitudes shown by these ectopic plants, isn't just due to "being caged" in relict locations, but also a relative adaptation with the time to these ecological conditions, unusual for the species. Indeed they prove to be resistant, vigorous and rather easy in cultivation, whilst nearly all the high altitude *S. wulfenii* plants are difficult and often "stunted" when grown at sea level, especially with an oceanic climate.





So it would seem that the houseleeks of Riegersburg and Herbertstein are a differentiated ecotype of *S. wulfenii* subsp. *wulfenii*, and their physiological (ecological) differentiation is associated with a clear tendency to produce hairs. However, in our opinion, this is not enough to justify a different nomenclatural treatment of these plants, that we consider to belong to the subsp. *wulfenii*.

Sempervivum wulfenii subsp. **juvanii** (Strgar) Favarger & J.Parn.

Sempervivum wulfenii subsp. juvanii (Strgar) Favarger & J.Parn. in J.Parn. & Favarger, Notes on Sempervivum L. and Jovibarba Opiz in Chater A.O. Flora Europaea. Notulae Systematicae, Sér. 2 n°3, in *Botanical Journal of the Linnaean Society*, 103(3): 217 (1990)

Basionym: Sempervivum juvanii Strgar, in Bioloski Vestnik, Ljubljana, vol. 19: 83-91 (1971)

Completely and constantly hairy-glandular plant. The epidermis is less glaucous than that of subsp. *wulfenii*, its grey colour being only due to the dense hairiness. The leaf basal blotch is generally well marked. Also, the stolons of this subspecies are often in greater number compared to the subsp. *wulfenii*, although this character seems more evident in cultivation than in the wild.

S. wulfenii subsp. juvanii is a very punctual, well characterized, endemic form, that grows on the Subpannonian mountains east of Slovenia. This morphologically very homogeneous population, is geographically very isolated from the rest of the species' distribution range. It only grows on two small twin volcanic reliefs (Donačka Gora and Resenick, their highest point being at about 880 m a.s.l.), isolated in the middle of a large calcareous massif. These reliefs are densely covered by forest, so this plant grows exclusively in the few vertical, rocky openings, very brittle and unstable. The plant starts at 500 m a.s.l., but the highest concentration can be found between 700 and 850 m. Its entire distribution range is no larger than a few hundred square meters and local conditions (very closed environment) don't allow the plant to expand outside its current range. It's clearly a very rare and vulnerable plant, made by a single population with a low number of individuals (some dozens, a few hundreds maximum). Although they are at low-altitude, access to the micro-locations of this species is difficult and dangerous: the majority of plants can't be reached without climbing gear, and this is their best protection.





Its geographical isolation, its marked hairiness compared to the *wulfenii*-type (very glabrous) and more important, the very low altitude of its stations (*wulfenii*-type being clearly a plant of high altitude), would lead to consider this taxon as a distinct species, as it was initially described by Vinko Strgar, Curator of the Botanical Garden of Ljubljana [in *Bioloski Vestnik* XIX: 83-91 (1971)]. However, this Slovenian houseleek is clearly related to *S. wulfenii* Hoppe for various reasons:

... its vegetative morphology, almost identical in the two taxa, except for the hairiness;

... the floral morphology, practically identical;

... the identical chromosome number, 2n = 36;

...the preference for the same substrate, the two plants being strictly acidophilous.

The identical chromosome number (2n = 36, diploid) of these two plants, as well as the presence of the above-mentioned intermediate locations in the southeastern Alps (see above), these locations being unknown to Strgar at the time of the publication of *S. juvanii*, urge now to consider *S. juvanii* a well-differentiated subspecies of *S. wulfenii* rather than a distinct species.

This point of view (one same species) is reinforced when comparing the relationship between the low altitude Austrian *wulfenii* (see above) with *S. juvanii*, which is distinguished by *S. wulfenii* for 1) its evident leaf hairiness, 2) its isolated ectopic distribution range, 3) its low altitude localization.

Relation of subsp. *juvanii* with the intermediate populations of subsp. *wulfenii*

As already analysed, the houseleeks at Riegersburg and Hebertstein can be considered, for many reasons, as more or less intermediate between *S. wulfenii* and *S. juvanii*, not only for their geographical position, but for their morphology and ecology too. Similarly to *S. juvanii*, they grow at low altitude, whilst the distance between their habitats is a little more than 80 km as the crow flies, so that the plant of Riegersburg and Herbertstein represent a relative geographical, morphological and ecological *continuum* between *S. wulfenii* and *S. juvanii*. For this reason, it's difficult to maintain a specific status for *S. juvanii*, whilst it seems more logical to consider it as a well characterized local population of *S. wulfenii*, of which it can be seen as a subspecies.

Although partially distinct too, morphologically and ecologically, compared to *S. wulfenii*-type, the houseleeks at Riegersburg and Hebertstein can't be directly linked with the subsp. *juvanii*. Their general aspect, their glaucescence, the apparent nakedness (their hairiness, if present, can be appreciated only after careful examination, whilst it's quite evident in subsp. *juvanii*), make them immediately indentifiable with the subsp. *wulfenii*. Caution: Not too much importance should

be given to the small individualization of these Austrian Styria plants: their differences with the *wulfenii*-proper morphotype are just details in our opinion, and only the existence of the *juvanii* morphotype and it's geographical proximity, give some importance to these details, and this is why we insist on the subject.

Particularly isolated, and lacking the possibility of genetic exchange with the alpine populations and even with the nearest Austrian Styria populations, the small, Subpannonian population of *S. wulfenii* became autonomous and has differentiated, facilitated by being very small and well delimited (with possibly the appearance of "founder effect"⁽²⁾ or non-adaptive variations phenomena⁽³⁾). All this has promoted the individualization of the subspecies *juvanii* as we know it now. It should be pointed out that perhaps the hairiness of these plants shouldn't be considered as a secondary differentiation, but, more likely, as the persistence (or maybe the accentuation) of and ancestral character of juvenile type.

Random variation not caused by modification of the surrounding environment and without slective consequence.



The founder effect is a process where, i.e. after a long period of isolation, a small number of individuals, carrying only a fraction of the genetic variability of the original population, start a new population.

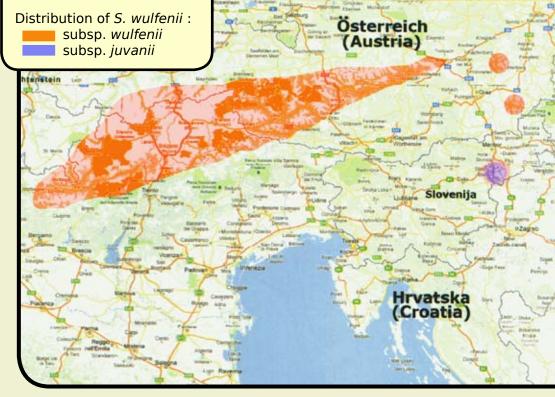
Distribution

Sempervivum wulfenii is an endemic species of the wide range constitued by the eastern Alps, the Styrian Prealps and the Subpannonian Mountains. A good part of its distribution range is located in Austria, whilst in Switzerland it can be found in the south-east of the Grisons only. In Italy it's abundantly present in the dolomitic region on crystalline and effusive rocks, and in several localities west of the river Adige valley, up to the provinces of Sondrio and Bergamo.

Although it can't be considered rare in Nature, *S. wulfenii* only rarely forms large populations, but is rather present here and there in well distinct places, these local populations being sometimes dense. These populations are frequently mixed and widely surrounded by a great quantity of hybrids (see below), mainly with *Sempervivum montanum* L., another high altitude houseleek that is almost constantly in company of *S. wulfenii*, except in its eastern locations at low altitude.

The subsp. *juvanii* shows an ectopic location compared with the whole of *S. wulfenii*, being its southernmost representative. Its minuscule distribution range is completely isolated and very far from the species' main distribution range: the siliceous central-eastern Austrian Alps. Not to be forgotten the low altitude punctual stations (relict stations) which have been treated above in this text, representing a sort of dotted bridge between the heart of the distribution range and this extreme localization. From a geographical point of view, we can't speak of a distribution range broken in several well distinct areas, but we can't ignore the presence of evident gaps in the south eastern part either.

All the low altitude populations of *S. wulfenii* in the south-eastern part (Mürtal, Riegersburg, Herbertstein, Donačka Gora and Resenick, ...) should be probably interpreted as post-glaciation relicts: being the high altitude regions of the Alps unsuitable for their survival during the quaternary glaciations, representatives of the ancestral branch of *S. wulfenii* were pushed away by the ices and formed stable colonies at the southernmost limit of the Alps and in the rare crystalline sites of the mainly sedimentary south-eastern Prealps. The isolation of some of these shelter areas have subsequently lead to a certain differentiation, as indicated by the subsp. *juvanii*.



It should be mentioned that S. wulfenii has often been confused, in floral compendia, with Sempervivum grandiflorum Haw., another yellow-flowered houseleek, acidophilous too, but evidently having a very different aspect (we'll discuss it in a next article). On the contrary, confusion between S. wulfenii subsp. wulfenii and S. tectorum var. glaucum (Ten.) Dalla Torre & Sarnth. during the vegetative stage is more understandable, although that shouldn't happen if the plants are carefully examined (see description), furthermore they can't be confused during the flowering period. The possibility of this confusion with S. grandiflorum or S. tectorum, explains why some stations (obviously doubtful) well to the west of the classical distribution range, are often indicated in literature. The western boundary of S. wulfenii remains hence relatively uncertain, situated between the lake of Garda and lake of Como. We have personally confirmed its presence up to the Val Venina, in the Sondrio province, and near Carona, in the Bergamo province.

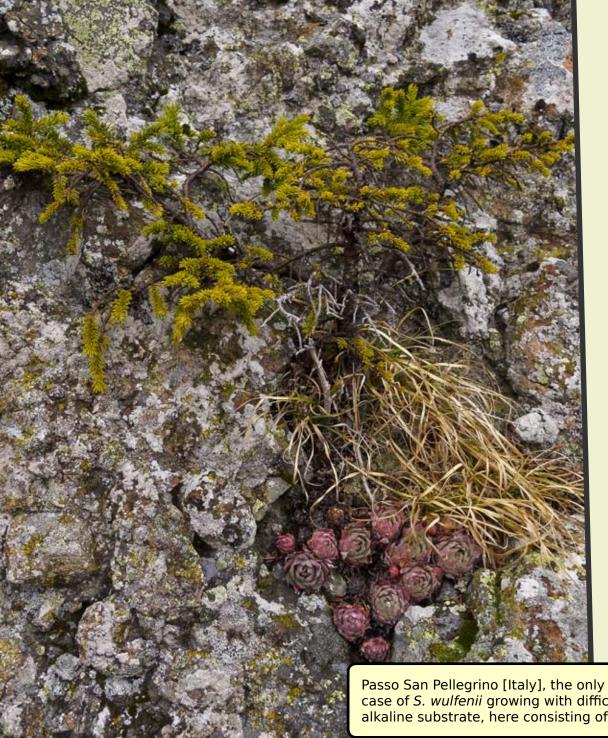
Ecology

S. wulfenii is constantly a heliophilous and acidophilous species and almost constantly a high altitude plant.

Due to its marked **heliophily**, probably even higher than the majority of houseleeks, it can be exclusively found in really sun-exposed stations. Whilst many high altitude houseleeks like or even seek the partial shade offered by low bushes (*Juniperus* for example) during the hottest hours, *S. wulfenii* accepts full sunshine only or just a slight and temporary shade, preferring like the majority of the houseleeks at these latitudes, a south-east exposure, facing the morning sun, in other words. This strict heliophily is a reality for the subsp. *wulfenii* but is less marked for the subsp. *juvanii* which seems to better accept light shade *in situ*, in such conditions it etiolates a few but maintains itself.

Its <u>acidophily</u> is equally strict. Almost all the currently known natural stations of *S. wulfenii* are on siliceous rocks (crystalline or volcanic). In those massifs where crystalline "islands" emerge from sedimentary rock (the Dolomites for example), *S. wulfenii* exclusively grows on these islands, almost completely absent elsewhere in that area. The only exception to this rule it's the presence (personally verified) of a few colonies currently growing at the Passo San Pellegrino (Trento, Italy) on dolomitic ground, but the small size of the rosettes proves that the plant is not finding the optimal conditions for its growth on this substrate.





Its preference for **high altitudes** (alpine and subalpine levels) is clear. Unlike the other common species on the Alps, like S. tectorum or S. arachnoideum, the altitudinal range occupied by this species is rather narrow: S. wulfenii is not normally encountered at medium and low altitudes (mountain and hill belts).

Its ecological needs, as far as the acidophily and altitudinal range, seem to be comparable to those of S. montanum, with which it often cohabits, although its distribution it's obviously more punctual than *S. montanum*: the latter is ubiquitous at high altitudes on the Alps, whilst S. wulfenii generally forms dense, but limited and scattered populations, rather than large areas with merging borders like *S. montanum*. The small populations of S. wulfenii are generally surrounded by a wide "cloud" of hybrids, as already said, the one with S. montanum being the most frequent. At the moment, we are unable to explain which is the factor that limits *S. wulfenii* in well defined areas, whilst all around it the ecological conditions seem to be the same, and are full of its hybrids. There are still many things to uncover on the houseleeks' physiology and ecology.

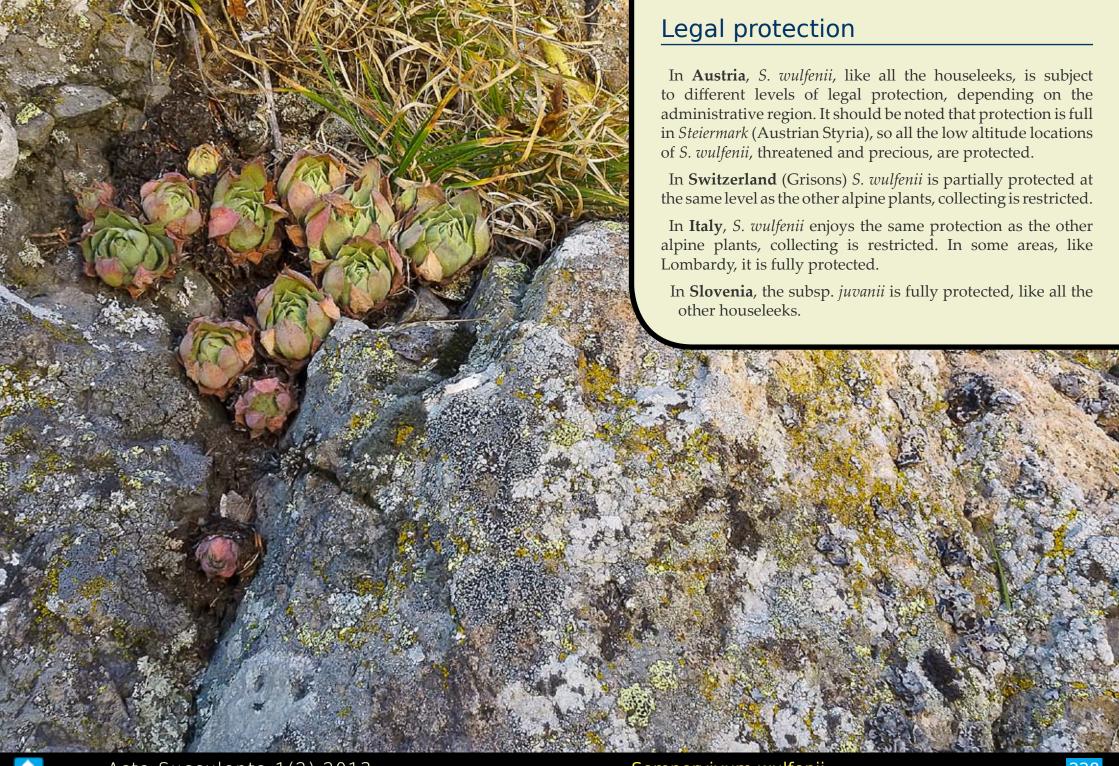
Further on the altitude topic, what we said earlier applies to the vast majority of the distribution range - the core of the Alps – but, as already reported, doesn't in its south-eastern margins. In the Austrian Styria, there are a few real low altitude populations, below 1000 m a.s.l. (the lowest just at 500 m, at Riegersburg).

Passo San Pellegrino [Italy], the only known case of *S. wulfenii* growing with difficulty on an alkaline substrate, here consisting of dolomite.

What can we gather about the history of this plant?

The existence of very isolated and ectopic locations at the south-eastern border of the Alps, well known to host many alpine plants in a relict post-glaciation situation, leads to think that these stations of *S. wulfenii* are shelter-stations too, for any of their characteristic. In addition, the plants they host, show a certain individualization ranging from moderate (Autrian Styria) to evident (Slovenia). The existence of relict stations, the absence of species directly connected with *S. wulfenii* in the genus *Sempervivum*, the scarcely morphologically evolved stolons, as well as the rather low chromosome number (2n = 36, diploid, when the genus *Sempervivum* is characterized by a high chromosome number, sometimes very high, with many polyploid taxa) lead to think that *S. wulfenii* is a rather ancient species in a rather young genus, this latter still undergoing an active speciation process, with, as a consequence, rather imprecise specific limits.

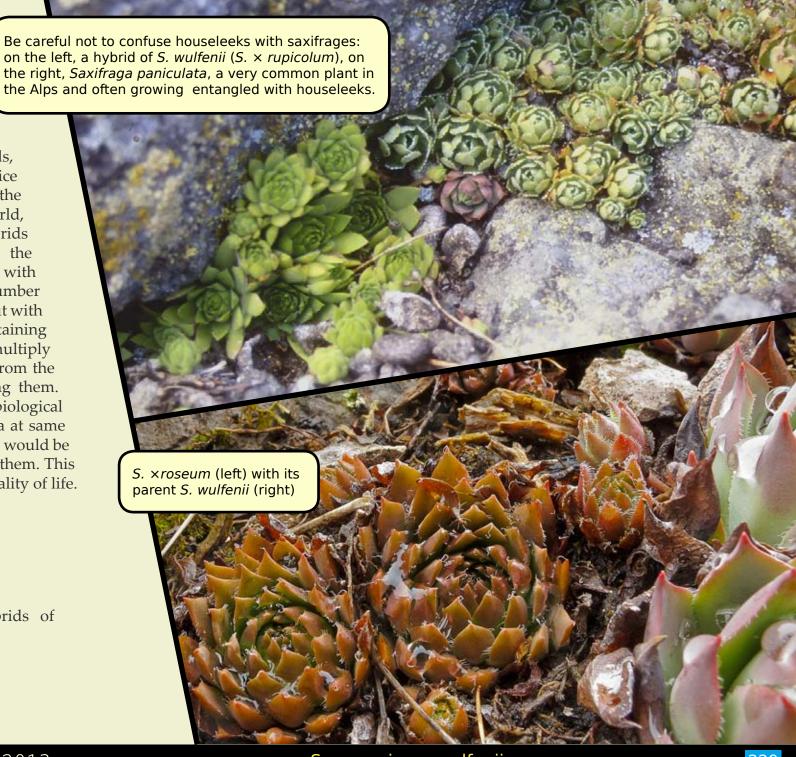




Natural hybrids

The majority of succulent plants growers dislike hybrids, even natural hybrids. This prejudice is really counterproductive for the understanding of the houseleeks' world, since in a natural population, hybrids are often more numerous than the parent species: we are not dealing with the occasional plants, in a limited number and having difficulties to survive, but with real populations, capable of maintaining themselves during time and to multiply in the long period, independently from the parent species, sometimes replacing them. These hybrids are thus authentic biological entities and therefore authentic taxa at same level of their parents, so much that it would be stupid to attach a different value to them. This is the extraordinary and complex reality of life.

These are the inter-specific hybrids of *Sempervivum wulfenii*:



Sempervivum ×rupicolum Kerner (S. montanum × wulfenii)

Sempervivum ×rupicolum Kerner, in Oesterreichisches Botanisches Wochenblatt Gemeinnütziges Organ: 285 (1870); and in Zeitschr. Ferdinandeums Tirol., Innsbruck, ser. 3, 15: 270 (1870)

syn.: Sempervivum ×theobaldii Brügger

Sempervivum × *rupicolum* is by far the most frequent amongst the natural hybrids of *S. wulfenii*, considering the almost constant cohabitation of S. wulfenii and S. montanum. S. ×rupicolum is the predominant element of the "cloud" of hybrids that generally surrounds every station of S. wulfenii. It is therefore far from being a rare plant.

The rosettes of *S.* ×*rupicolum* are more similar to *S. montanum* than to S. wulfenii, but the colour is often a very pale green, yellowish sometimes, whilst its tall flower stalk resembles more that of S. wulfenii than the short one of S. montanum. This flower stalk is therefore very long and heavy compared to the rosette' small size and, as a consequence, is often flexed at its base. The flowers are easily recognizable for their peculiar beige colour.

So, identifying *S.* × *rupicolum* in Nature it's rather easy: if you encounter a "S. montanum" with pale leaves and a tall stalk bearing beige flowers in the eastern Alps, it's certainly a *S.* ×*rupicolum*. However, it's important to point out that some rare individuals have purplish flowers, similar to those of S. montanum (in the Sempervivum genus, the red colour of the flower is frequently dominant over the yellow colour in some hybrid individuals, whilst in others it appears like an intermediate colour). There's no other difference between the specimens with a beige flower and those with a purplish flowers, so that nothing leads to believe that the latter are the result of back-crossings of *S. ×rupicolum* with *S. montanum*, but without certainty.





This hybrid is classically divided in two nothosubspecies, matching the subspecies of S. montanum, which has two well characterized subspecies (in our opinion, a differentiation to the specific rank of *S. montanum* subsp. *stiriacum* could be asserted, but we'll discuss this on another occasion). The parent's clear-cut morphological difference isn't passed fully to the hybrids:

Sempervivum ×rupicolum subsp. rupicolum

Coincides with the hybrid *S. montanum* subsp. *montanum* × *S. wulfenii*.

Sempervivum ×rupicolum subsp. pernhofferi (Hayek) D.Donati & G.Dumont

Sempervivum ×rupicolum subsp. pernhofferi (Hayek) D.Donati & G.Dumont, in Piante Grasse 36(2): 42 (2012)

syn.: Sempervivum ×rupicolum n-var. pernhofferi (Hayek) G.D.Rowley

Coincides with the hybrid *S. montanum* subsp. *stiriacum* × *S. wulfenii*.



Sempervivum ×**roseum** Huter & Gander (*S. arachnoideum* × *wulfenii*)

Sempervivum ×roseum Huter & Gander, Die Alpenflora der österreichischen Alpenländer, Sudbaierns und der Schweiz, Lindauersche Buchhandlung: 121 (1899)

flowering period (at the same altitude, S. montanum starts to flower earlier than S. arachnoideum). Its rosette is relatively small and open, with a few short arachnoid hairs on the S. $\times roseum$: as in S. $\times rupicolum$, the long leaves' apex, the flower stalk is tall and bears nice flowers with long pale-pink petals, flower stem is disproportionate to the size sometimes slightly beige tinged, although, in our personal experience, we have of the rosette and often leans down under never seen specimen with beige flowers comparable with those of *S. ×rupicolum*. the effect of its own weight. Caution! A clone often named "Sempervivum roseum" is present for a long time in cultivation. It's a small indestructible and very prolific plant of unknown origin and imprecise nature, but one thing is certain: it is not *S*. × *roseum*!

Sempervivum ×roseum is the second hybrid in order of frequency of S. wulfenii,

although decidedly less common than *S.* ×*rupicolum*, it's even relatively rare. In addition, since its aspect is less characterized than *S.* ×*rupicolum*, it can be sometimes

confused with the commonplace *S.* ×piliferum Jord. (*S. arachnoideum* × tectorum).

Its lesser frequency is probably due to the shorter overlap of the parent species'

Sempervivum × widderi C.B.Lehm. & Schnittsp. (S. tectorum × wulfenii)

Sempervivum ×widderi C.B.Lehm. & Schnittsp., in Berichte Offenbacher Vereins Naturkunde 1: 36 (1860)

S. *widderi is the rarest of S. tectorum hybrids, for two reasons: at first, the cohabitation of S. wulfenii and S. tectorum is rather sporadic, since S. wulfenii often grows at higher altitudes than S. tectorum, in addition, it's very difficult to distinguish this hybrid during the vegetative stage due to the strong resemblance between the two species. Even during the flowering period, distinguishing this hybrid isn't easy, since some populations or clones of S. tectorum have very pale off-pink flowers, not very different from the dull light beige colour of the flower of this hybrid. As a consequence, identify a houseleek like S. *widderi by simply observing its morphology is at most a likelihood, and a karyological confirmation is often necessary to be affirmative.

This has a two-fold consequence: on one hand the real frequency of this hybrid is probably underestimated due to the difficulty in recognizing it, on the other hand, the majority of cultivated plants under this name are just large forms of *S. tectorum* or cultivars with unknown lineage...



Sempervivum ×alidae Hort. ex Zonn. (S. grandiflorum × wulfenii)

Sempervivum ×alidae Hort. ex Zonn., in British Cactus and Succul. Journal 4(3): 65 (1986)

This hybrid is reported here just for completeness, since it's an artificial hybrid, created in cultivation. It's really unlikely that it could ever be found in Nature, since the parent species don't cohabit (*S. grandiflorum* is a typical species of the Piemonte and Valle d'Aosta Italian regions). This epithet is nomenclaturally valid, but needlessly clutters it, so it would have been best to publish this taxon as a cultivar, because it's nothing more.

Sempervivum dolomiticum × wulfenii

This hybrid has been only recently discovered at the Passo San Pellegrino (Italy/Dolomites). On this subject, see the article by Mariangela Costanzo in *Cactus & Co* 1/2006,

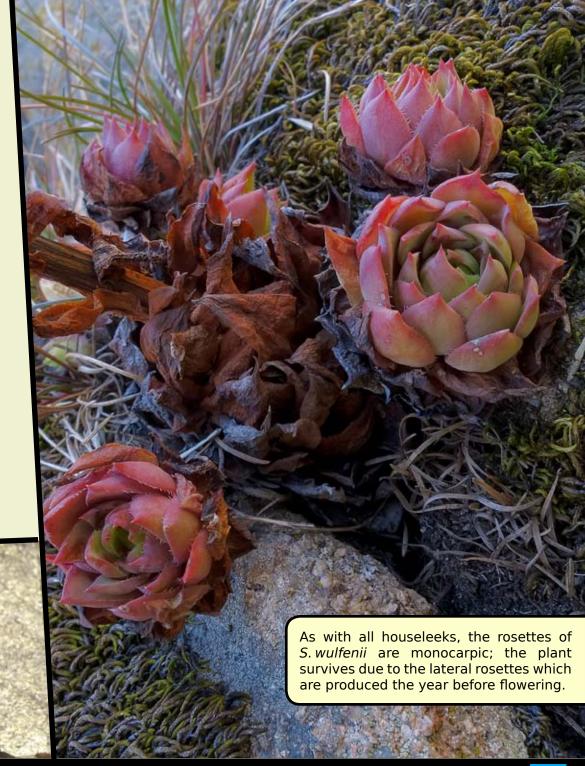
Its presence has been hypothesized as the result of anthropic activities: some rosettes of *S. dolomiticum* could have been transported, together with dolomitic material, near colonies of *S. wulfenii*, allowing the crossing between these two plants that have so different ecological needs, and normally don't share their habitat. It isn't possible to say as yet whether this hybrid will disappear or it will be capable of taking hold and increase its numbers in the long period. Recent visits to the habitat seem to highlight a numerical regression of this hybrid.

Cultivation notes

Sempervivum wulfenii isn't the easiest houseleek in cultivation, being very sensitive to winter humidity, which mandates protecting it from rain starting from autumn even in areas with continental climate, or worse, oceanic climate. Its high altitude habitat implies some sensitivity to hot summer temperatures coupled however with a real hunger for sunlight. It's thus advisable to position it east-facing (or north-east in hot areas) during summer, in order to give it at least 6 daily hours of full sunshine (minimum) but avoiding it to cook in the afternoon.

Like any other houseleek, *Sempervivum wulfenii* isn't afraid of frost, it benefits from it actually, provided it hasn't started to etiolate, something that can easily happen when cultivated at sealevel. Regular, but well spaced waterings, are useful during the spring-summer to avoid damages by "dog-days".

In cultivation, *Sempervivum wulfenii* is rather slow-growing and scarcely prolific: it will never form large, opulent clumps made by many rosettes, for this reason it's better grown in pots rather than rocky gardens. This will help protecting it from humidity if necessary, and better appreciate its beauty. *S. wulfenii* isn't a houseleek useful for mass effect, but rather for close examination.





Variability depending on provenance

Clones originating from the few low altitudes relict localities are easier to cultivate than those from the high areas of the Alps: often more vigorous and prolific, they have a markedly higher endurance to hot weather. They are hence often nicer in cultivation than their high altitude cousins, but like them they are very sensitive to winter humidity.

In the frame of the species, the subsp. *juvanii* represents an extreme from any point of view: morphological, geographical and altitudinal. Its cultivation is no exception: this plant is probably one of the most vigorous houseleek in cultivation, but unfortunately it's also one of the most sensitive to humidity, and can rot as quick as it grows. Even in the middle of summer, just a period of prolonged rain can be enough to considerably damage its rosettes, and keeping it alive during autumn and winters is rather difficult, at most in areas with an oceanic climate, and even with a continental climate. However, when rot sets in, its great vigour allows to keep it by restarting even from a tiny fragment escaped from rot. Provided the tiny fragment is saved...

As far as the various hybrids of *S. wulfenii* are concerned, they inherit from their parent some sensitivity to humidity and a rather few exuberant growth when cultivated at sea-level.

Propagation

Propagation of *Sempervivum wulfenii* can be easily done by transplanting the lateral rosettes in any draining substrate, better if fairly rich (enriched with some leaf mould). Considering the stolons' thickness and persistence, allowing the cut to dry-up for a few days it's advisable.

Sowing is possible but scarcely adopted.

Where and how to get Sempervivum wulfenii?

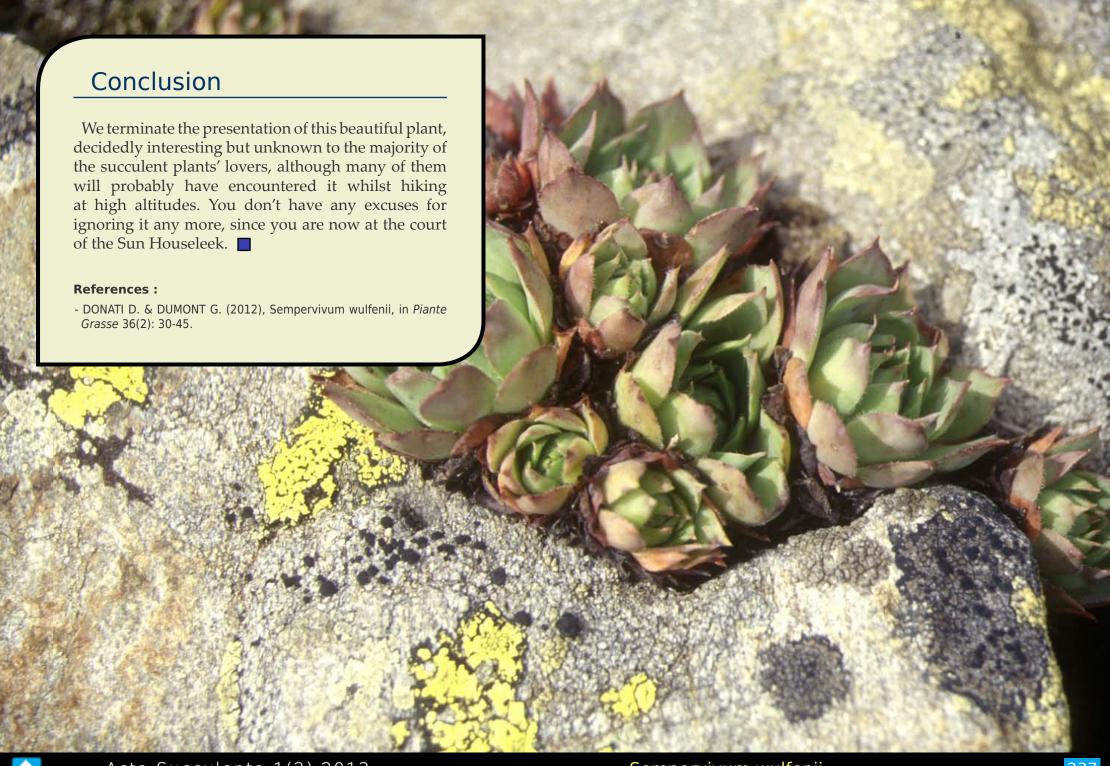
Sempervivum wulfenii can be found in most nurseries catalogues of hardy succulents and Alpine plants. The subsp. juvanii is more rarely offered, but remains relatively easy to find.

Hybrids of *S. wulfenii* are more difficult to get, not because of their availability, but because you can't be really sure of their id and you'll get anything and everything under apparently correct names...

The low altitude plants from Styria (Mürtal, Riegersburg, Herbertstein) seem to be absent on the market. It's a pity because they are the nicer in cultivation. However, considering that the majority of the commercial clones of *S. wulfenii* lack locality data, that these Styrian plants are the easiest to grow, and that growers concentrate on easy plants, it's quite possible that they are already available somewhere. Apart from this, the plants from Styria with locality data are already in many collections, and their owners are often happy to swap them with other amateurs.







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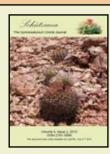


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