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Travelogue of a photographer and a naturalist, (part two).



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two little known
Fouquieria.



Inula crithmoides, the false Crithmum who dreamed of being a true one.



WIG: Succulents with style!



Sempervivum montanum, a jewel from the high peaks.



EDITORIAL



I have been in Mexico, again.

Again, the incredible hugeness of Mexico City, so big you can drive for hours on the highways which cross the city.

Again, the stillness of the small towns "lost"in the middle of the Chihuahuan Desert.

Again, the fantastic hospitality and friendliness of the Mexican people.

Again, on the skin the unforgettable, burning Mexican summer.

Again, the roadrunner crossing the track.

Again, male tarantulas walking incessantly, looking for a female.

Again, the wonderful, silky flower of echinocerei.

Again, the spines of corynopuntias in the skin.

Again, the astonishment at the incredible strength of tiny cacti like Turbinicarpus, Pelecyphora, Ariocarpus... able to survive in such a harsh environment.

I've enjoyed my time again - how strong life is there.

But this time I've seen something else.

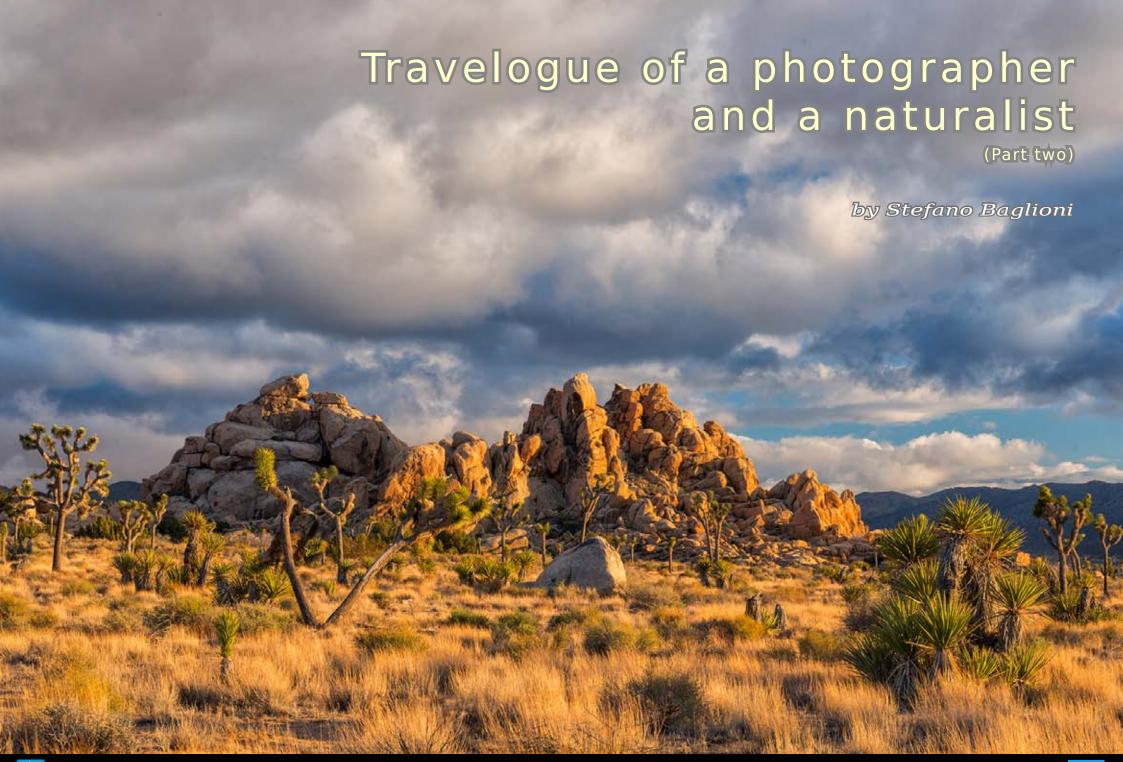
Guns, rifles, grenade launchers, bazookas... entire States where it was strongly recommended to stay away for safety reasons.

Army and police massively involved against narcotraffic.

I've had two machine guns pointed at my face.

Good luck Mexico, for a better future.

DAVIDE DONA



These words should bring to mind boundless lands, unforgettable sunrises, snow-capped mountains...

Instead, they make me think of the passenger seat.



Yes, because "the passenger" was really my role for hundreds and hundreds miles, in a car which was running fast across the vast and beautiful region of the Great Basin: a land of contrasts and colours, where snow-capped mountains emerge from scorching deserts, where strange spiny lizards flee to the human footstep, but above all a land where Davide coveted to arrive.

Yes, because the time to take photos freely was over, it was time to search: we were in the realm of the protagonist of his research (probably he had palpitations), a succulent plant, or better a *Cactaceae*, strange and beautiful at the same time in his complicated structure.

Micropuntia pulchella (Engelm.) M.P.Griff., I was worried even by its Latin name...

Eastern Great Basin

my mind was already working on the best way to take a picture of this

See: S. Baglioni (2014), Travelogue of a photographer and a naturalist (part 1), in

Here we go! I took a last look back, as a greeting to Arches NP⁽¹⁾, while unknown plant (at least for me), I was trying to visualize its size, its shape, the best lens to take a shot... in short, the usual ruminations by a common photographer who doesn't know anything about plants.



Davide, feeling my uncertainty, tried to describe this cactus with words and gestures, but the more I listened him, the more I wondered if the hard nights spent without sleep had some after-effects on him: he spoke about napiform roots (?) cylindroid segments sometimes annually deciduous (?), acicular and sometimes papery spines (?), glochids... It was interesting to listen him, but every time I tried to visualize this cactus in my mind, thanks to these unfamiliar terms, the result was always quite worrying.

The first stops were not very edifying for my friend: the *Micropuntia* was absent. Then a sort of continuous buzz followed him, asking incessantly: "Is this one your plant?", "Is this one the plant you are looking for?", "So is this the one?", "Anyone else would have felt bothered, fortunately Davide replied calmly: "No, it's *Escobaria vivipara* (Nutt.) Buxb., we have already seen it before", "No, it's *Pediocactus simpsonii* (Engelm.) Britton & Rose", "No, it's Opuntia hystricina Engelm. & J.M.Bigelow", "Noo, that's Sclerocactus pubispinus (Engelm.) L.D.Benson, I told you that my plant is composed of many pieces attached together." In short, I had no idea about what we were looking for...









Fortunately, as proof of the Italian saying "When you are looking for something, you find something else" we met a wonderful lizard, the American collared lizard. What a beautiful animal, some shots were a must!

We drove for some tens of miles, then we stopped and Davide called me very excitedly, a few steps out of the car: "It's here". In front of me, two stubby and reddish sticks sprouted from the gravel, half dried up, with some spines here and there: honestly the first impression was not so nice, I hadn't any ideas that could enhance this plant in a picture...

"Don't worry, this is the plant described by Daston as Micropuntia barkleyana; actually this is a suffering specimen, the next one will be beautiful!" Davide was trying to reassure me.

Although the next specimens were certainly more attractive, honestly this tiny cactus was not able to inspire me as many other succulents which I met during the trip. I was forgetting that I was in the Great Basin, a land with extreme contrasts, a place where the climate is terrible, where every inch of growth represent a strong effort even for the hardiest of plants. I tried to show this difficulty in my pictures. We were concerned by one thing however: due to late cold weather, all the plants of *Micropuntia* were full of well developed buds, but they weren't ready to bloom yet. Although the period was perfect (at least on paper), it seemed that we were missing the flowering by a few days.

The disappointment was getting a foothold....

So we were again into the car, I was back once more in my dear passenger seat ("the passenger", do you remember?), maybe we could be so lucky as to find a specimen in flower in the next place.

The more we drove for miles and miles across the Great Basin, the more the contrasts became evident: the desert alternated suddenly with green areas rich in animals and plants, where even woods were present. There you can even see low, snow-capped mountains silhouetted on torrid plains, an unbelievable experience: the temperature was 35 ° C and the sunlight was scorching, but in front of our eyes we had snow.

Finally! STOP!

I was fascinated by that landscape, which had the essence of the Great Basin inside, at last in my opinion: the typical sagebrush (Artemisia tridentata) in the foreground, snowcapped mountains in the background and the beautiful, warm light of the sunset.



we hadn't found «Her» in her heyday, that is, a or rather the enormous amount of miles we had flowering Micropuntia, but no problem, we had to drive: nothing new, Davide had tried the thrill a lot of time to spend there (i.e. I had to hold on of the life of the photographer before, now I was to my passenger seat for a lot of miles). Before tasting the life of the researcher.

I was tired and a little disappointed because bedtime, we discussed the route for the next day,







Northern Great Basin

The next morning came soon after a restful night: breakfast, a talk with the owner of the motel (he deserves a special chapter) and... Let's go!



Each stop corresponded with a surprise, at least for a photographer like me: at the first stop, a very nice horned lizard (Phrynosoma hernandezii) ran away, not far from a Micropuntia. Alas, also in this region the plants showed nice buds, but no flowers, although they belonged to "another taxonomical group of Micropuntia" (Davide dixit). Davide was beginning to be worried, the plants would have been blooming in a few days, but we hadn't so much time...

Another day was ending, but Davide was happy again, thanks to the discovery of a huge form of *Micropuntia*: over 40 cm in diameter and up to 20 cm tall, with spines almost 10 cm in length, a giant compared to other forms we saw, which generally do not exceed 10 cm in diameter and height.



So I learned that this plant was described by Curt Backeberg with the name of *Micropuntia wiegandii*; few people were lucky enough to observe it in habitat. Well done, Davide!

The area was very dry and arid, we had spent too many hours walking under a blazing and clear sun which had almost "cooked" our skin, but I was feeling I was on Mars, so a picture of the sunset was a must....



Central-western Great Basin

Nothing new that day: endless straight roads, beautiful landscapes and many *Micropuntia*, so many that Davide was surprised by their abundance; unfortunately bad luck was following us and we were not able to find a single flowering plant. What a pity...

At a junction, I won: we moved the research to a not so good place for *Micropuntia*, but perfect for the needs of a photographer. So we drove the car (or rather, Davide did, I was almost one with the passenger seat...) to the County of Mono, we were to spend the night on the banks of the famous Mono Lake. I wanted to remedy the first disappointing day of my trip: I didn't get a decent picture.



I was tired and hungry, the unhappiness was arriving. Eight slices of bacon cooked on the open flame of a small fire, 4 sandwiches and 2 beers were the remedy: with a full belly, everything looks better.

It was time for a little deja-vu: I was going to spend the night in the car, waiting for the sunrise on the lake; then the research again, a flowering *Micropuntia* was surely waiting for us somewhere. Something was new, instead: Davide was so tired that I was not able to wake him up after 5 calls, slamming his tent vigorously and even honking! I desisted, impossible to wake him up, I photographed the sunrise alone.







Central-southern Great Basin: Her

We were searching for a flowering Micropuntia, yet in each place we only found plants in bud. That morning, however, the weather was stable, a little cloudy but the temperature was constantly over 30°C: each place could be the right one. We stopped on a hill just above the highway and... intuition, what a good thing!



I had in front of me the protagonist of the story as recounted by Davide some days earlier, surrounded by the extreme nothingness, in every sense. Only the deafening noise of the giant trucks, which sped past nearby, disturbed us.



This plant is extraordinary: small, aggressive, very hardy, but at the same time it's extraordinarily delicate when it's showing its silky, magenta flowers. I could forget everything of that trip but not "Her", and if you're wondering why I'm calling that *Micropuntia* as "Her", the answer is easy to give: the story by Davide, the research, the anticipation for a blooming plant, its amazing flowers, and also sleepless nights, canned beans eaten on the roadside, discussions, but above all that stop, which seemed to me lost in time, instead we found the only site where the micropuntias were in bloom... "Her" deserves my maximum respect now.



The search was almost at an end, Davide was able to think about the collected data, while I was almost able to engage with him in a vague discussion about the "morphological changes" (!!!) of *Micropuntia pulchella* across the region of the Great Basin. I was aware about the adaptation of a plant to all the variation of its habitat, so that in the following months, no longer affected by the "photographic anxiety", I realized day by day how fascinating were those endless hours spent with only one goal: *Micropuntia pulchella*.





Back to Mojave: Death Valley

Our time was ending, we only had a few days before our return, but on the way to Los Angeles we had to cross the majestic Death Valley, a very famous depression below sea level placed in the middle of the desert; an area unique for its extreme climate, with strong seasonal and daily thermal excursions.



We arrived there at dusk, the light was perfect for a picture, but very high temperatures still inflamed the crude territory, burned by a scorching sun. While the car was going into the depression... "Careful!! Don't squash it with the wheels!". We avoided by a whisker a long snake, probably a gopher snake (Pituophis catenifer) with fantastic colours. What a fantastic day!

Unexpectedly (but not so much, this place is the "valley of the death"), at 8:30 PM the temperature was almost 40°C, I tried to take few photos at sunset and a few intimate shots of this lunar landscape, including also the only car driving in that nowhere land, but I had a lot of problems, since it's hard to work in such temperatures. It's hard to believe that some cacti are able to live there without problems (at least appearently), for example *Echinocereus engelmannii* (Parry ex Engelm.) Rümpler, *Opuntia basilaris* Engelm. & J.M.Bigelow, but above all *Echinocactus polycephalus* Engelm. & J.M.Bigelow, majestic even in places where no other plant can grow.

When you have a late dinner with a temperature around 40°C, everything appears little strange and difficult, especially if you have to cook something on a small fire; but a sandwich with roasted bacon is so good that you soon forget anything is wrong.

We needed energy and a little rest, since we had to spend the entire night sleepless, under the bright Great Bear.

What? Why am I speaking about a constellation?

Well, you'll understand when you read the last part of this article.

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to be continued..





in order to describe very particular succulent plants which inhabit dry areas in Mexico and the USA: the members of this genus have semi-succulent to succulent bodies, covered with prickly, thin and rigid spines which project directly from the stem. The development of the spines of *Fouquieria* species is quite unusual: the leaves of these plants which sprout directly from the younger portions of the stem have the outer side of the leaf petiole thickened and quite lignified. Once the leaf dies, the inner (upper) part of the petiole falls together with the leaf blade, but the lower, woody part remains, forming the spine.

The genus *Fouquieria* is presently composed of 11 species. They are plants which typically grow in open or rather bushy areas, on flat or gentle slopes, generally on gravelly and sandy soil.

Two little-known species are worthy of mention for their very particular ecology, which appear almost at poles apart. We are speaking about *Fouquieria leonilae* Miranda and *Fouquieria shrevei* I.M.Johnst and we report here our field experience with these plants.

Fouquieria leonilae Miranda

Fouquieria leonilae Miranda, in *Bol. Soc. Bot. México* No. 26: 127, tab. 128 (1961)

Typus: leg. F. Miranda, nº 9273, 1960-01-19; "Mexico, Guerrero: Cañon del Zopilote, cerca de Venta Vieja (Carretera Mexico-Acapulco) en selva baja decidua de latera de barranca lateral al Cañon"; HT: MEXU, IT: US.







Description

Fouquieria leonilae is a very interesting member of the genus Fouquieria: it's a shrub, generally 2 m tall, up to 4 m, with a rather thin (up to 15 cm diam.) long trunk, quite succulent and soft, green, with a very thin, almost papery cortex. The branches are few, thin, distributed along the stem, above all on the upper portion.

This species is remarkable for having the smallest spines of the genus, blackish-grey and almost invisible in some plants.

Leaves are oblanceolate, up to 5 cm long.

The flowers of this species are quite distinctive: a long raceme with sparse flowers appears at the top of mature stems (or at the leaf axils close to the apex); the gamopetal, quasi-salver-shaped corolla is blood red coloured, with a very long conical tube and short lobes. This structure indicates that this species is strictly adapted to hummingbird pollination.

The fruit is a capsule containing many elongated seeds, with well developed membranous expansions.





Distribution

Fouquieria leonilae grows in the central Balsas Depression in the Mexican Guerrero State, exclusively in the Zopilote Canyon; a wide, rocky valley. The habitat is distributed in little more than 20 sq km.

Ecology

Fouquieria leonilae grows in dense, deciduous tropical dry forest, among bushes and trees, at an elevation of 400-600 m a.s.l. It closely resembles the Bursera and Jatropha shrubs and trees that it grows with, and the distinction between them is very difficult above all with young plants.

Fouquieria leonilae appears highly saxicolous or rupiculous, since plants grow mainly on rocky slopes and almost vertical cliffs, where they rarely exceed 2 m, or among dense vegetation on scree slopes, where 4 m tall plants aren't rare.

Other succulents in the area: Mammillaria guerreronis (Bravo) Boed., Neobuxbaumia mezcalaensis (Bravo) Backeb., Agave aff. petrophila, etc.



Fouquieria shrevei I.M. Johnston

Fouquieria shrevei I.M.Johnst., in *J. Arnold Arbor.*, 20(2): 238 (1939) [pro *Fouquiera*]

Typus: leg. I.M. Johnston, n° 7815, 1938-09-20; "Mexico, Coahuila: 26 km S of Laguna del Rey, on road to Mohovano, on gypsum-flat"; HT: GH.





Description

Fouquieria shrevei is very interesting member of the genus: it's a shrub up to 2-3 m tall, with a very short trunk which branches repeatedly; these branches are thin and long, often inclined or even horizontal near their base, then erect, giving the plant a typical candelabrum shape. The new portions of the stem are whitish-grey, and the old portions possess vertical resinous wax bands, orange-amber coloured, and rough to the touch. The older the plant the thicker the resinous layer.

Spines are strong and very prickly, whitish-grey, distributed on the entire stem.

Leaves are ovate to oblanceolate, up to 3 cm long and 2.5 cm wide, with scarious, often dry margins.

The flowers of this species are unusual for the genus: short racemes of small and short white flowers bear in the axils of the leaves along the stems, they are scented and probably moth-pollinated; the rest of the species in the genus produces flowers at the top of the mature branches, which have long, tubular corollas and are generally pollinated by hummingbirds or carpenter bees (*Xylocopa* sp. or similar). Young plants of *F. shrevei* at 50 cm tall, can flower.

The fruit is a capsule containing 3-4 seeds. Seeds are small compared to the rest of the members of *Fouquieria*, 2-4 mm, white, roundish and rather thick, with short membranous expansions.







Ecology

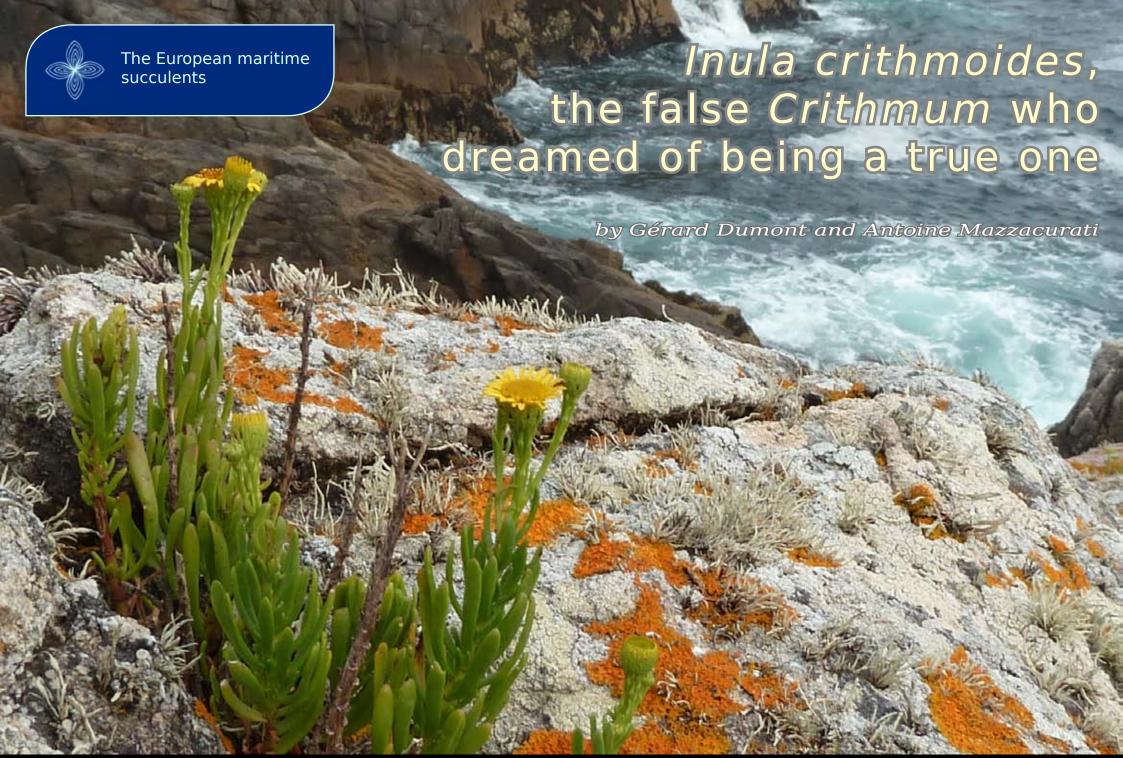
Fouquieria shrevei grows at an elevation of about 700 m up to 1100 m asl.

This species is extremely gypsophillous; it's specialized to grow only on soils with a high concentration of gypsum, on the flat and up to quite steep slopes. It grows very rarely on other kind of soils, where it's supplanted by *Fouquieria splendens*. These species grow often very close one to each other, showing a distinct ecology, without any evident hybrids.

Other succulent plants associated: *Neolloydia conoidea* Britton & Rose, *Epithelantha greggii* (Engelm.) Orcutt, *Echinocereus* aff. *stramineus*, *Yucca rigida* (Engelm.) Trel., etc.









The started this series⁽¹⁾ on maritime succulent plants with one of the most representative of this type of plant, one that that come first to the mind of any person who knows the European coast: Crithmum maritimum L. This is also the plant that came first to the mind of the great Linnaeus when he had to name the plant that we now present to you: Inula crithmoides L., i.e. the false Sea samphire.

This poor plant was very upset to be so relegated to the background, playing the role of an imitator, with its ever so pretty yellow daisies while its model is unable to produce anything other than banal greenish carrot-like flowers. She would so like it that this cumbersome pretention was renamed with something like *Crithmum inuloides* but, alas, no botanist thought so.

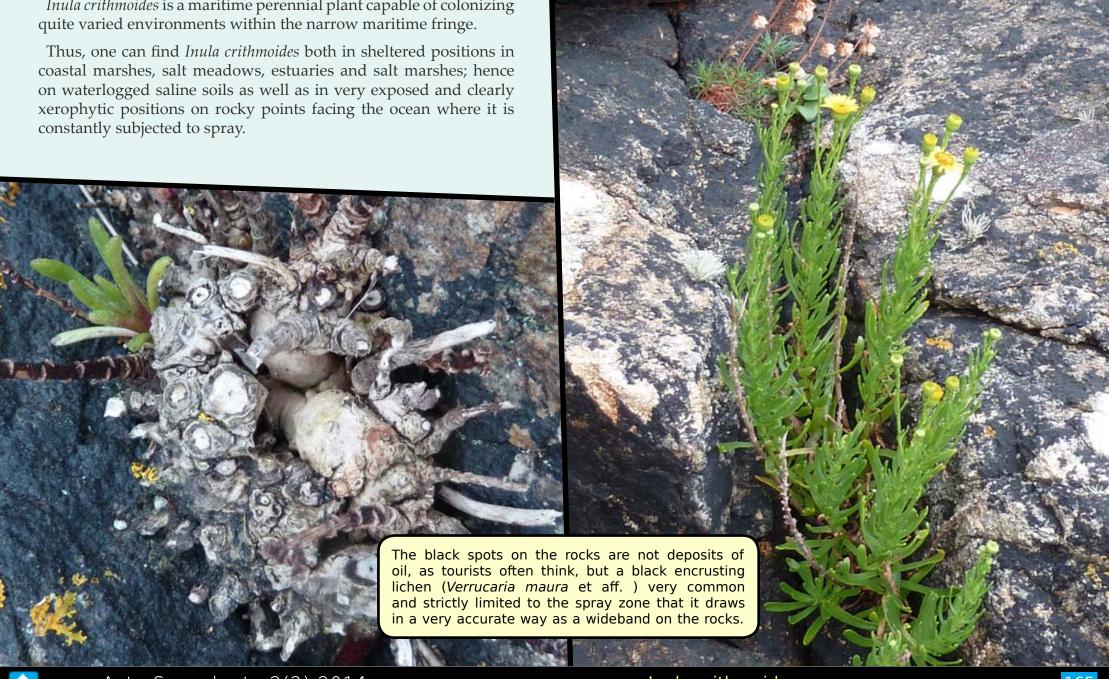
So we do it justice here...

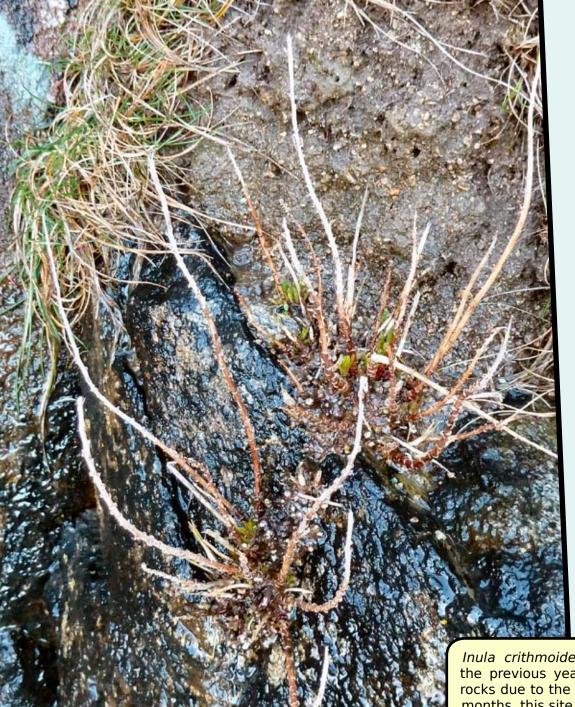
¹ G. Dumont & A. Mazzacurati (2013), Crithmum maritimum, The succulent of storms, in *Acta Succulenta* 1(1): 23-51.



Ecology

Inula crithmoides is a maritime perennial plant capable of colonizing





Although it can colonize dry places, *Inula crithmoides* is more a plant that can easily withstand a transient drought rather than a plant that seeks it. This is easily seen in its stations in rocky areas, where it prefers to settle in moist cracks and areas of seeping rocks. Note, however, that in most cases they are non-permanent seeping areas, very wet in winter but often very dry in summer. This observation seems totally discordant with the growth cycle of the plant, which is clearly a summer grower. Its predilection for such sites may be explained by the fact that they facilitate its implementation in improving the rate of survival of its seedlings whose germination is late and occurs when the rain comes back in autumn and therefore when the rocks start to seep again.

Inula crithmoides also doesn't dislike settling into the fringes of the aerohaline lawns of fescue⁽²⁾. In this kind of site, the salinity of the substrate is generally rather low, but the salt intake by the wind are still regular and high.

Inula crithmoides rarely makes large diffuse populations, spread all along the coast, but rather make spots scattered here and there. Some of these spots may be relatively large but they generally have precise limits. In these spots, the density of the plant is very variable, sometimes sparse and clearly dominated by its companion plants, sometimes dominant (on some seeping rocks).

Inula crithmoides in late winter (the stems of the previous year are dead) on seeping vertical rocks due to the percolation of rainwater. In a few months, this site will be very dry.

The abundance of fescue lawns in coastal environments with the rocky slopes of the Atlantic zone shows once again the parallel between the mountain flora and vegetation and the maritime flora and vegetation

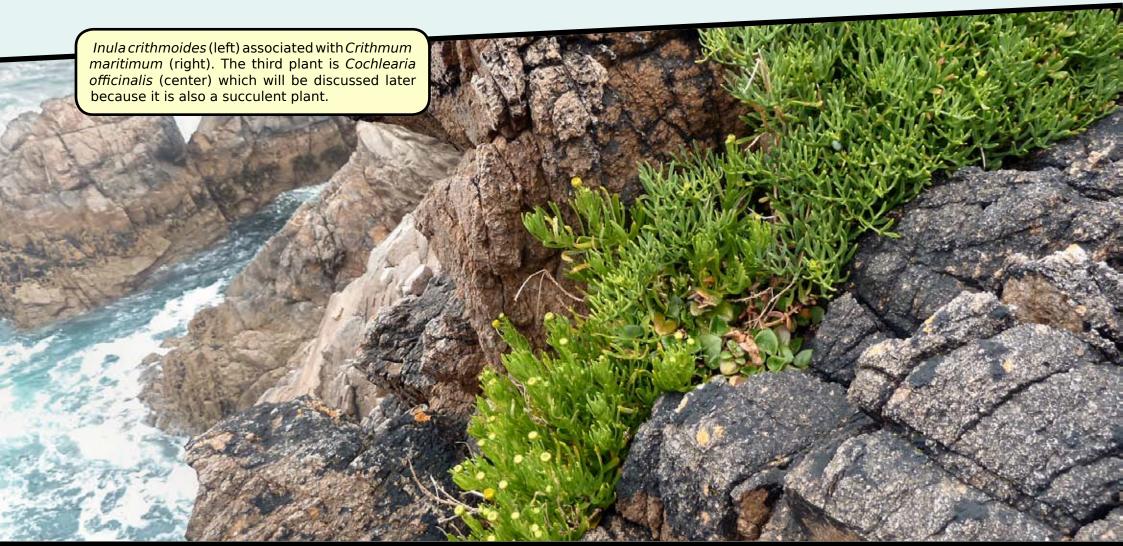
When the false one meets the true one...

On the rocky points housing *Inula crithmoides*, the type of habitat and the lifestyle of this plant are the same as those of *Crithmum maritimum*, of which we have already spoken in detail, that is to say, those of a saxicolous and rupicolous⁽³⁾ chasmophyte, indifferent to the nature of the substrate and whose habitat is limited to the spray zone. Inside the spray

3 "Saxicolous": living on rocks. "Rupicolous": living on more or less vertical rocky walls. "Chasmophyte": plant living in cracks.

zone, *Inula crithmoides* however goes less lower down to the water than *Crithmum maritimum* and prefers the middle part of this zone.

In rocky habitats, *Inula crithmoides* is almost constantly associated with *Crithmum maritimum* (but the reverse is not true) and these two plants often grow intermingled, the true samphire generally dominating the false one in terms of numbers in these mixed populations, although the opposite can sometimes be observed locally, but much more rarely.





Although sharing the same ecological niches, Inula crithmoides seems a bit more heliophilous and especially more thermophilous than Crithmum maritimum. This thermophily must be qualified according to the maritime nature of the environments occupied by these two plants: these environments are necessarily much less hot and with lower thermal amplitudes⁽⁴⁾ than the sites further inland. In its locations in rocky or semi-rocky environments, there is a relative predilection of Inula crithmoides for rocks facing south and southwest (without it is an absolute rule) and for every area whose configuration allows them to store heat or benefit from reflection of solar radiation, such as flat spots at the foot of a wall. This is clearly seen in the Atlantic zone, certainly less in the naturally warmer Mediterranean area.

Thermal amplitudes of the maritime zones are highly attenuated compared to the zones just a few hundred meters inland and, a fortiori, to the remote zones of shoreline. This concerns both the annual amplitude (the difference between the average temperatures of the summer and the winter is low and the peaks of minimum and maximum temperature are very attenuated) and the nycthemeral amplitude (the difference in temperature between day and night is very low, the temperature variations of the substrate by the sunshine and the dissipation by nocturnal radiation predominate in this case over the temperature changes of air masses).



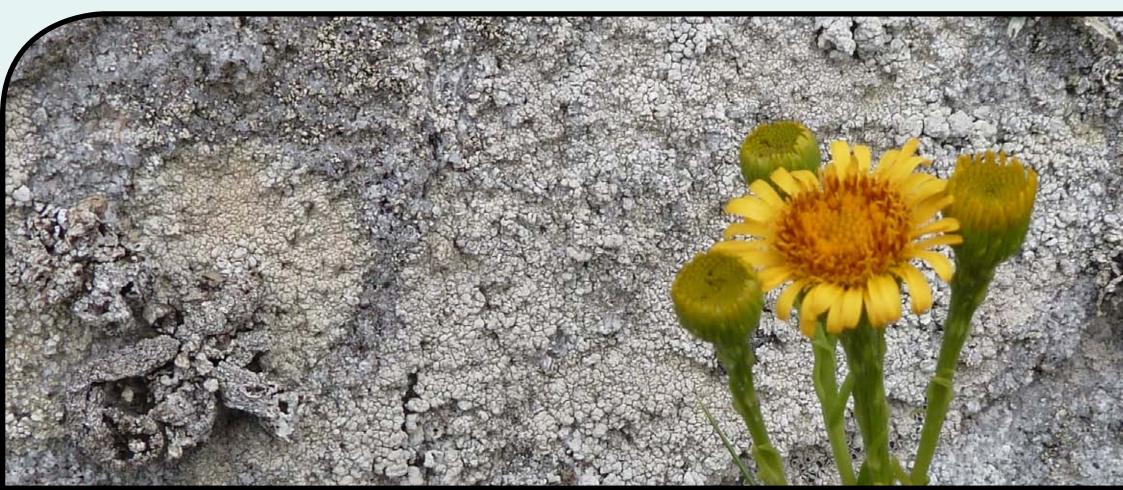
A Home loving behaviour

Although *Inula crithmoides* is only encountered, save for exceptional cases, in marine environments and in close proximity to water, it does not show any special adaptation to this environment with respect to its mode of dispersal. Indeed, its seeds, which are light and equipped with a tuft of feathery hairs are only scattered by the wind (such a plant is called anemochorous), as for nearly all the *Asteraceae*, and it produces no real propagules that can be transported by sea. While its short lateral branches can sometimes be torn away from the stems and then eventually root remotely, it seems a rather accessory way of dispersal because these branches don't break off easily in the wind and their leaves are too soft to withstand the violence of transport by waves and splashes against the rocks.

In coastal areas, the local prevailing winds generally blow from sea to land or from land to sea (thermal winds reversing day/night) but more rarely parallel to coastlines. This probably causes a difficulty for this strictly anemochorous plant living very close to the water, to spread its seeds laterally along the coast. This perhaps explains the many gaps in its area, which consists of a multitude of very localised spots scattered along the coastline. These gaps are apparent even in seemingly favorable zones in which the absence of the plant is difficult to explain by environmental constraints. It is likely that the vast majority of seeds of this plant are swept away and wasted either inland or seawards and only a tiny minority happen to germinate in a favourable environment. Besides, sexual dispersal is the only one possible for this plant, which has no mechanism of vegetative dispersal.



The relative difficulty of dispersing and implanting itself is demonstrated not only by the "dotted" aspect of its locations along the coast, but also by the relative scarcity of young seedlings *in situ*. The consequence of this is that, unlike many plants of the maritime rocks, and, more generally, unlike many maritime plants, *Inula crithmoides* doesn't behave clearly as a pioneer plant. It seems to implant itself with a bit of difficulty in virgin or disturbed environments and hence will have difficulty in recovering the space eventually lost.





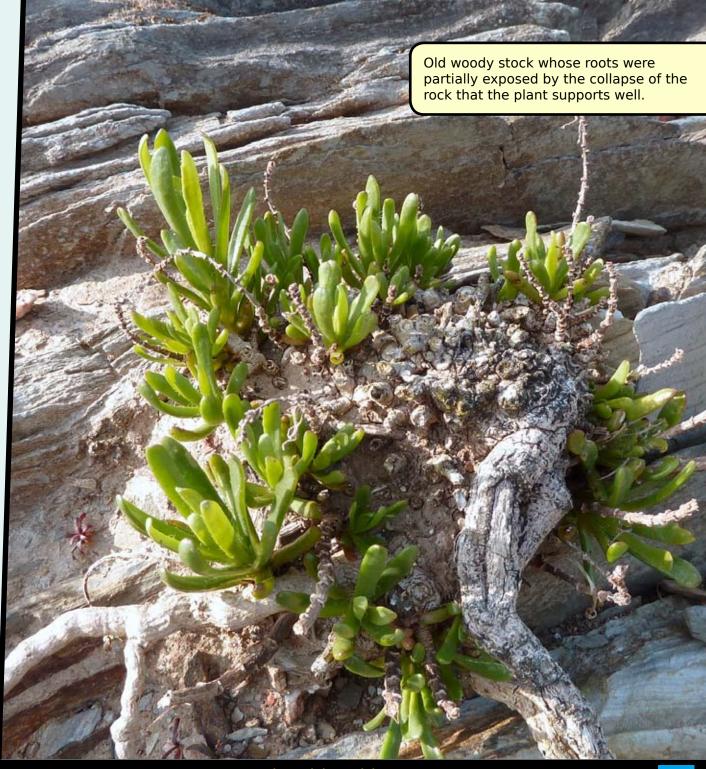
This lack of a pioneer nature is certainly the explanation why *Inula crithmoides* often grows less near the water than *Crithmum maritimum*: physiologically it could do so, as it does in sheltered areas, but on the lower parts of rocks of which the vegetation is periodically destroyed by winter storms, *Crithmum maritimum* can quickly regain the lost space but *Inula crithmoides* hardly does. This is also the reason why *Inula crithmoides* is quite rare in much frequented rocky sites and often absent in strongly anthropized areas, unlike *Crithmum maritimum*.



A tough plant

This seemingly difficult dispersal and implantation is not a great problem for the maintenance of this plant because it is balanced by the high strength and durability of the plant once established. Indeed it appears that the locales of *Inula crithmoides* are particularly stable from one year to the next: few or no new plants but few or no losses. Even in late winter, it is rare to find any dead individuals. On the matter of longevity, it is difficult to know precisely what age an individual can achieve in situ but in each location the stocks looking very elderly are numerous (in a particularly hostile environment for plant life, don't forget that).

With Inula crithmoides being particularly tough and long-lived, a low multiplication rate is sufficient to ensure the perfect balance of its populations. But this high resistance of individuals paradoxically makes populations fragile to any changes in their environment. Any decrease in numbers of a population will be difficult and slow to recover and then the plant may be replaced by some other plants with more efficient colonizing abilities. Conversely, the presence of Inula crithmoides is usually a good indicator of a stable and healthy maritime environment (though again we should not make an absolute rule).





A true maritime plant

Although the dissemination strategy of *Inula crithmoides* remains that of a "continental" plant (anemochory, little or no vegetative propagation), on the other hand its morphological and physiological adaptations to the maritime environment are very neat and efficient:

- Obvious halophytism: high tolerance to saline soils, but no real halophily (salt is tolerated but is not necessary for the plant).
- Succulent leaves as an adaptation to summer drought and high osmolarity of the substrate.
- High mechanical and physiological withstanding of wind and spray: the stems do not break, leaves resist without damage the regular salt deposits.
- -Ability of the rootstock to creep into rock cracks and firmly anchor the plant inside them.

From an evolutionary point of view, it is generally considered that reproductive organs and mechanisms evolve more slowly than morphological characters because they are less subject to the selection pressure than vegetative organs. If one adheres to this theory, often confirmed by observation, it should be seen in *Inula crithmoides* a plant having conquered the maritime environment relatively recently, and in any case more recently than some other plants that we presented to you earlier in this series. However, more than a conquest it is more likely a speciation *in situ* because this plant is absent outside the maritime fringe and it does not have near continental parents.





Description

Plant: perennial, branched from the base, with stems at first erected and very stiff but able to bend secondarily, suffrutescent with woody base, about (20-)30-80(-100) cm tall. The long stems (auxiblasts) produce in their leaf axils many very short leafy branches with condensed, almost virtual internodes (brachyblasts), which give the plant a densely leafy appearance, these short branches may lengthen slightly (a few centimetres) at the end of the season. The main stems (new auxiblasts) appear from the stock that is thick, tortuous and woody.

Leaves: alternate, fleshy, glabrous, bright green, sessile, linear to slightly obovate-cuneiform, ending obtusely or inconsistently with three teeth and sometimes marked with a red spot with indistinct limits; winter leaves are shorter, linear-cylindrical, with blunt untoothed apex. Slightly aromatic foliage.

Flowers: grouped in hermaphrodite heads with a central domed disc and ligules radiating, disk and ligules are plain yellow, diam. circa 2-3 cm; the heads are grouped in lax corymbs of heads successively flowering, the stalks of the heads are abundantly covered of bracteoles. Blooming attracts many insects (entomophilous pollination) and runs from early summer to early autumn in the Atlantic zone, with a maximum in July, but can spread over most of the year in hot Mediterranean areas.

Fruits: achenes with pappus, grouped in dense reddish-brownish pompoms. Staggered maturity depending on the flowering date.



Possible confusion

In the vegetative state, confusion can possibly occur *in situ* with *Crithmum maritimum*, because of the similar appearance of the two plants and their common locations (sea rocks).

In bloom, any confusion between these two plants is impossible. However, at this moment *Inula crithmoides* can be confused with the Cape groundsel (*Senecio inaequidens* DC.), an invasive *Asteraceae* of South-African origin but whose appearance is much more slender and although it enjoys coastal areas it does not grow in a strictly maritime situation.

In the salt marshes, *Inula crithmoides* can, from a distance, be confused with another *Asteraceae*: *Pulicaria dysenterica* (L.) Bernh, which is also present in these places, but being less halophytic and less maritimal than *I. crithmoides*, it is especially common in wetlands behind the maritime area. Both plants have relatively similar flowers and general habit but in close-up the resemblance fades because their leaves are very different.



Variability

The variability of *Inula crithmoides* is mainly phenotypic, linked to environmental conditions, plants in sheltered situation (salt marshes, etc..) being less stocky, less succulent and producing less brachyblasts than those in exposed situations (sea rocks).

There is however a real intrinsic variability, which is mainly expressed by the length of floral ligules⁽⁵⁾, the length and width of leaves, the frequency of tricuspid leaf apex of the more or less glaucous leaves. This variability does not seem sufficient, in our opinion, to recognize real infraspecific taxa in this species and taking that into account (cf. infra: *Nomenclature*) is more a convenience of classification than a factual reality.

The length of the ligules varies from half the diameter of the central disc to the value of this diameter, i.e. a length which varies from one to two. Nb.: ligules are the «petals» of *Asteraceae*, each ligule is a single flower, as each floret which together constitute the central disk.







Distribution

Inula crithmoides is relatively common on all European and African coasts of the Mediterranean, including the islands. It is also quite common on all European coasts of the Atlantic and the English Channel up to Normandy (Calvados dept.). Further north, it remains present on the west, south and south-east coasts of the British Isles but it becomes rare and sporadic on the east coast of Britain.

Inula crithmoides reaches its absolute northern limit in southern Scotland and its southern limits on the Atlantic coast of northern Morocco (southwest limit) and the Mediterranean coast of Egypt (southeast limit).





Uses

Inula crithmoides is an edible plant whose young leaves can be eaten raw or cooked or as a soup. Their taste is tart and rather pleasant and unlike *Crithmum maritimum*, the harvest season has little influence on the eating quality.

The three maritime succulent plants that we have previously discussed in this series⁽⁶⁾ were also edible plants, and among those we will present in future issues, some will be too. You might think that, at this rate, in a few issues, your favourite journal will become a culinary magazine... Don't worry, we always prefer admiring plants to eating them. At least, we take the time to observe them before eating them...

In fact, edibility must be differentiated from culinary interest. Among the maritime succulent plants, only a few of them actually have one and it remains modest; they are more often condiments than true vegetables. Some fans of "natural food" nevertheless even today show some interest in *Inula crithmoides*.

The edibility of many maritime succulent plants only reflects the extreme poverty in the past of many coastal regions (now it is quite the opposite) and most of these edible plants were once only famine foods, some particularly foul, we must admit.

In the absence of great gastronomic qualities, *Inula crithmoides* nevertheless has real nutritional value, due to a relatively high protein content⁽⁷⁾ and secondarily in iodine, which would perhaps, after varietal selection, make it an interesting plant to grow on soils degraded by salinization. We have already discussed a similar context regarding *Cakile maritima*⁽⁸⁾.

⁸ G. Dumont & A. Mazzacurati (2014), Cakile maritima The traveller of the sands, in *Acta Succulenta* 2(1): 45-77.



⁶ Crithmum maritimum, Honckenya peploides, Cakile maritima.

⁷ R.A. Zuraykab & R. Baalbakib (1996), Inula crithmoides: A candidate plant for saline agriculture, in *Arid Soil Research and Rehabilitation* 10: 213-223.



Protection

In **France**, *Inula crithmoides* is fully protected at the regional level in the region of Basse-Normandie (Arrêté of 27th April 1995 updated 16th May 1995). This protection is motivated by the fact that the plant is there in the limit of its area on the southern coast of the English Channel.

In Italia, Inula crithmoides is protected in some regions by regional laws.

In **Spain**, *Inula crithmoides* is protected as plant "de interés especial" in the autonomous region Castilla-La Mancha (Decreto 33/1998, DOCM de 15 de mayo).







Notes of cultivation

Because of its rather wide ecological latitude, *Inula crithmoides* is easily cultivated in different conditions from its natural environment. Its Mediterranean origin for a large part makes it more resistant to heat than many other Atlantic and northern maritime plants.

Greenhouse cultivation is not suitable; it is too hot in the summer for a maritime plant even for a Mediterranean one like this. Cultivate it outside, in pots or in the ground. *Inula crithmoides* is very tolerant of drought but prefers nevertheless to have its feet in fresh soil, so don't hesitate to water thoroughly and, like most plants from salty soils, be heavy-handed with fertilizers.

The salt intake is not essential to the survival of the plant, but like all maritime succulent plants, they increase the succulence and natural aspect of the plant.

Inula crithmoides withstands moderate frosts; even if its foliage is damaged, its rootstock will survive. It is also advisable to cut off all the stems at the end of winter, the plant will be much more beautiful the following summer.

Inula crithmoides is not afraid of winter moisture, it is even necessary (it looks for it in nature)





Propagation

Inula crithmoides can easily be propagated by seeds or cuttings.

Sow the seeds as they mature. They are quite thin and equipped with a feathery pappus, it is not necessary to waste time removing it before planting.

For cuttings, preferably use the short lateral branches (brachyblasts) carried by the main stems.

How to get this plant?

Inula crithmoides is rarely offered in the trade, but it is however possible to buy it in a few nurseries specialized in seaside plants and some of them sell it on the Internet. This plant being fairly easy to propagate, it is generally cheap.

The plant itself is commercially available with a little searching, however its seeds don't appear to be (only the *Index seminum* of some botanical gardens offer them). To get them, you have to gather them in the wild in an area where the plant is not protected and you must be there at the right time because once ripe the feathery seeds fly away at the first breeze, like those of a dandelion...



A bit of nomenclature...

Inula crithmoides L., Sp. Pl., éd. 1:883 (1753)

Family: Asteraceae (nom. altern. Compositae)

Type: (Lectotypus) leg. anonym., s.n., sine loco, LINN 999.34 / design. Anderberg in *Taxon* 47: 363 (1998)

Synonymy:

- ≡ Jacobaea crithmoides (L.) Merino, Fl. Galicia 2: 337 (1906)
- ≡ Helenium crithmoides (L.) Kuntze, Revis. Gen. Pl., 1: 342 (1891)
- *≡ Limbarda crithmoides* (L.) Dumort., *Fl. Belg*.: 68 (1827) (non *Senecio crithmoides* Hook. & Arn.)
- = Eritheis maritima Gray, in Nat. Arr. Brit. Pl., 2: 464 (1821)
- = Inula crassifolia Salisb., Prodr.: 201 (1796)
- = Inula crithmifolia Wild., Sp. Pl., ed. 4, 3(3): 2101 (1803)
- = Limbarda tricuspis Cass. in Cuvier, Dict. Sci. Nat., 26: 438 (1823)
- = Senecio crithmifolius Scop., Fl. Carniol., ed. 2. 2: 163 (1772)

NB.: many authors prefer to name this plant by the binomial *Limbarda crithmoides*. The connection of the plant to the genus *Limbarda* Adans. rather than *Inula* L. is based on non-consensual taxonomic considerations⁽⁹⁾ and we prefer to retain the well known Linnaean name of this plant.

The generic name Inula would derive from the Greek ($v\alpha\epsilon w$, meaning to purge, and is related to the medicinal properties of some members of the genus. The specific name crithmoides refers to the similarity of the plant with $Crithmum\ maritimum$, morphological and ecological similarity since these both plants share the same maritime rocky biotopes.

Chromosome number: 2n = 18 (10).

¹⁰ G. Kamari & al. (2012), Mediterranean chromosome number reports, in *Fl. Medit*. 22: [211-]213-214[-232].



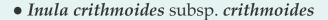
⁹ W. Greuter (2003), The Euro+Med treatment of Gnaphalieae and Inuleae (Compositae) – generic concepts and required new names, in *Willdenowia* 33: 239-244.

Common names

- (GB) Golden samphire.
- (FR) Fausse criste marine, Inule perce-pierre.
- (IT) Enula marina, inula marina, enula bacicci, bacicci.

Infraspecific taxa

Two broad geographical subspecies are generally recognized, the rationale for their individualization is mainly statistical in nature because at the level of isolated individuals it may seem somewhat artificial; many individuals of one subspecies can be identified as belonging to the other sub-species if there was no knowledge of their original location...



Synonymy:

 \equiv Limbarda crithmoides subsp. crithmoides

Atlantic regions.

Slightly cuneiform leaves, often with three teeth at the apex. Brachyblasts are abundant.



• *Inula crithmoides* subsp. *longifolia* Arcang.

Inula crithmoides subsp. *longifolia* Arcang., in *Comp. Fl. Ital*.: 371 (1882) [pro β. *longifolia*]⁽¹¹⁾

Type: [Inula acutifolia Pasq.] typus non designatus?

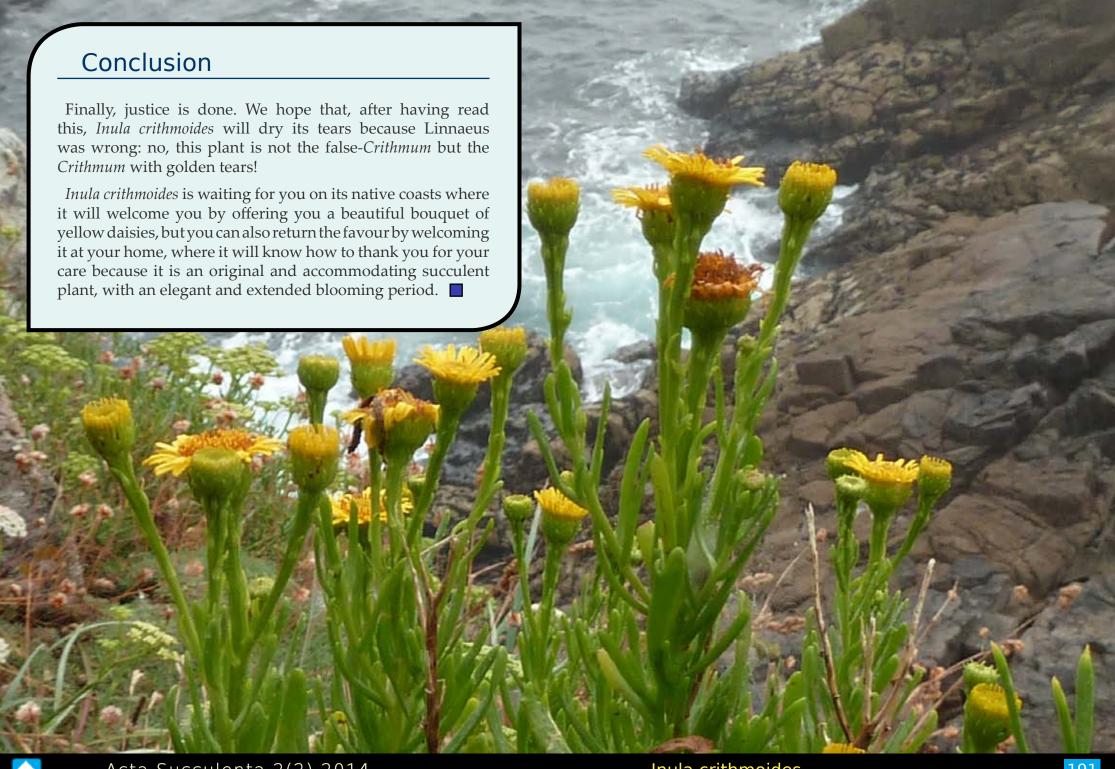
Synonymy:

- ≡ *Limbarda crithmoides* subsp. *longifolia* (Arcang.) Greuter, in *Willdenowia*, 33 (2): 244 (2003)
- ≡ Inula acutifolia Pasq., in Annali dell'Accad. Aspiranti Naturalisti, Napoli, ser. 3, 1: 19 (1861)
- = Inula crithmoides subsp. mediterranea Kerguélen in Blaise & al., in Lejeunia, n. s., 138: 5 (1992)
- = Senecio succulentus Forssk., Fl. Aegypt. Arab.: 149 (1775)

Mediterranean basin.

Leaves narrower and a little longer than the type, apex often toothless. Brachyblasts are less abundant than in the type.

The transcription in modern nomenclatural status of Greek letters to designate the infraspecific subdivisions, according to the ancient custom, is here contrary to the usage which is to translate them as synonymous with «varietas»; this letter is understood here as a synonym for «subspecies «because it is the usual interpretation of the status of this combination, we therefore follow it here, rightly or wrongly.







Was fifteen when I learned from my first teacher, Professor Giuseppe Lodi of the Botanic Garden of Bologna, the recipe for a good soil in which to grow succulents: field land clay, river sand and a small amount of beech leaf mold.

As he wrote in his famous book "Le mie piante grasse" (my succulent plants), he developed his solution by observing the photos depicting plants in the wild and trying to guess the composition of the soil trapped in the roots of imported plants.

The plants on those poor soils were growing slowly, but had a remarkable consistency and a beautiful, quite natural appearance.

It was 1979 and soon the market would be flooded with ready to use, organic substrates 'made for succulents'. The professional growers, of course, preferred to use such a light and inexpensive industrial product, in which the plants grew much faster.

Even I began to grow my plants in these soils, but the results did not convince me: I noticed the huge difference that existed between cultivated plants and those photographed in their habitat. The nurserymen commented on my observations claiming that it was all due to the Italian sun, much weaker than the Mexican one.

The turning point came in 1984, when I bought a plant of Aztekium ritteri on its own roots. It was obviously a wild specimen and I knew that there was little hope of keeping it alive. So I tried to give it a condition as similar as possible to the natural one: it was known that plants of this species grew mainly on gypsum and, fortunately, next to my house there was one of the most extensive outcrops of gypsum of the Apennines. I could then set up my first pot 'wildstyle' by placing fragments of natural gypsum in a pot to produce a composition where to put my plant. The result was satisfactory, since the plant began to grow very well and today it still reminds me how correct was that intuition!



A technical approach

After a course of scientific studies, which made me familiar with some important biological and ecological concepts as well as with geological ones, I was lucky to participate in an IOS session in Phoenix (Arizona) and I took this opportunity to get my first field knowledge by undertaking a large trip in the USA and Mexico with some important and well known experts on cacti and succulents. During this trip, I was able to observe the biotopes of interesting genera such as Ariocarpus, Turbinicarpus and Pelecyphora.

After one year I returned to Mexico in order to do populationa studies on Aztekium hintonii and Geohintonia mexicana, but also to collect some soil samples at various locations. These were then analysed at the Institute of Agronomy in Bologna, where it was found that those seemingly barren and arid soils were in fact, very fertile due to their clay component and the high content in nutrients.

Once back home, I busied myself with the study of geological maps of Mexico in order to understand the nature of those soils. I learned that the Sierra Madre Oriental, where the above mentioned species were widespread, was a mountain range originating from the lifting of the carbonate sedimentary rocks of marine origin in the Holocene era (about 30 million years ago).





This story was not new to me: even the Apennine chain that runs through Italy and on whose slopes is my own city, showed the same geological characteristics of the Mexican chain, being also the result of the lifting of carbonate sedimentary rocks of marine origin, although more recently (it was born during the Neocene, about 20 million years ago)

I then moved into the mountains in search of rocks similar to those I had seen in Mexico. It was not an easy search, because the Apennines are actually a complex system in which the autochthonous rocky component (the one I was looking for) is covered by a blanket of materials of different origin so-called 'scaly clays': a very malleable mixture of clay and limestone typical of bad-land formations, but in the end I was able to find a small deposit of sedimentary grey rock. As I learned later, that kind of soft rock mixed with clay was known as 'marl' and used in the manufacture of cement.





Soil, but also water, fire and air

I began to collect small amounts of the marlstone, which I used at first mixed with the organic potting soil, but later I preferred to use it pure, to re-pot a large number of cacti. I started with plants of the genera *Turbinicarpus*, *Ariocarpus*, *Pelecyphora*, and then moved on to *Mammillaria*, *Ferocactus* and *Thelocactus*.

For a naturalist like me it was obvious that the adoption of a soil similar to the original one could not, by itself, be sufficient to induce natural shape development, but that it was necessary to intervene on other ecological factors that affect the life of plants in nature and in captivity.

Water:

The plants were watered only seldomly, say once every 10 or 15 days in order to prevent rotting and death. Apparently no one considered the fact that the Mexican tropical latitudes are characterized by frequent torrential rainfall throughout the summer season, but obviously the widespread use of peat based substrates exposed cultivated plants to rot. Using natural mineral soil, that dries quickly, I could afford to break the rules and have taken to watering the plants whenever the soil appeared dry.

Sun:

More experienced growers argued that, in summer, the Mexican sun was so strong as to be impossible to reproduce, even by totally exposing the plants to our sun; despite this, those who possessed a greenhouse preferred to keep the plants under cover, also to avoid plants getting excessively wet with rain.

I began to think that the insolation difference between Italy and Mexico does not have to be so big: the summer rains, so frequent in tropical climates should cause a drastic decrease in the number of sunny days, compared to Italy where the summer is dry and sunny, so the annual energy balance between Mexico and Italy should not be much different. Another consideration concerned the intensity of light: the Mexican highlands were located at 2500 m above sea level, so that the light had to be much more intense than that of Bologna, which was only 60 m above sea level, so it became a priority to avoid using any filter (glass or polythene) to direct sunlight, and growing the plants in the open from spring to autumn.

Air:

The positive effects of open-air cultivation were not only those related to a better insolation: especially in spring and autumn, the plants thus grown benefited from a good daily temperature variation, just as they did in Mexico. This is important, because in these conditions, during the night the metabolism slows down and then the sugars produced by photosynthesis during the day is consumed in small part with night-time respiration. The same sugar may then be available by plants to synthesize cellulose and lignin, which constitutes hair and, especially, spines.



The results

Over the years, the plants that were cultivated with the wild grown style changed their appearance: grew much more slowly than the others, but their cuticles were thick and their epidermis had an intense colour. The spines of *Ferocactus* were finally similar to those of the fair creatures of the Mexican deserts and *Ariocarpus* plants stopped growing in height, and enlarged horizontally and developed massive root systems that destroyed the pots.



Wild Grown (WIG) plants, a choice of style

After years of experience I can now say that the WIG technique is well defined in its precepts and its application, even if the trial is far from over. I expect it can be applied to other kinds of succulent plants with different needs from the Mexican ones.





Wild Grown or WIG style

WIG (Wild Grown), is a style of cultivation aimed at influencing the development of succulent plants in order to let them take on the typical habitat appearance.

In principle it is the use of techniques of extreme cultivation, i.e. aimed at limiting the natural propensity of succulent plants grown in developing the soft tissue (aquifer parenchyma) and instead encouraging the production of dry matter (cellulose, lignin, cuticle, cork, wax, sugars, proteins etc.) through the use of poor substrates, cultivation in the open air and the drastic reduction of fertilizers.

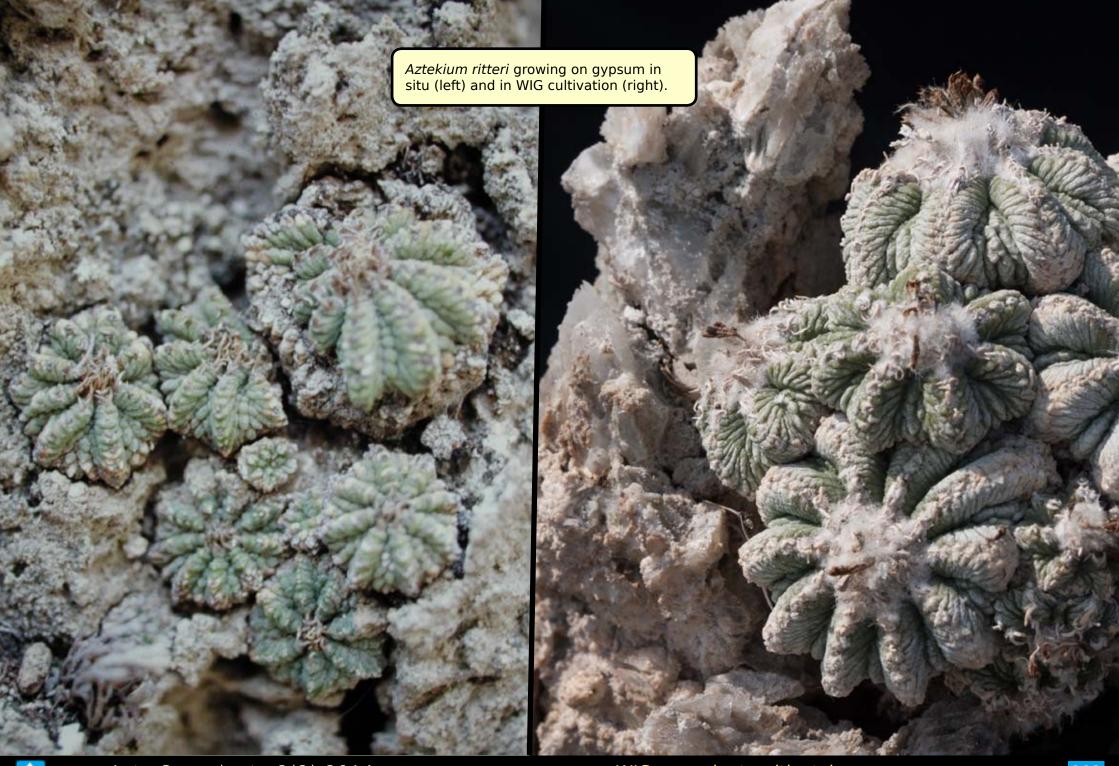
The plants obtained with techniques of extreme cultivation, as well as being similar to wild plants, show a clear accentuation of fertility, resistance to solar burning and extreme air temperatures (both high and low) and to aggression by parasites and infections.

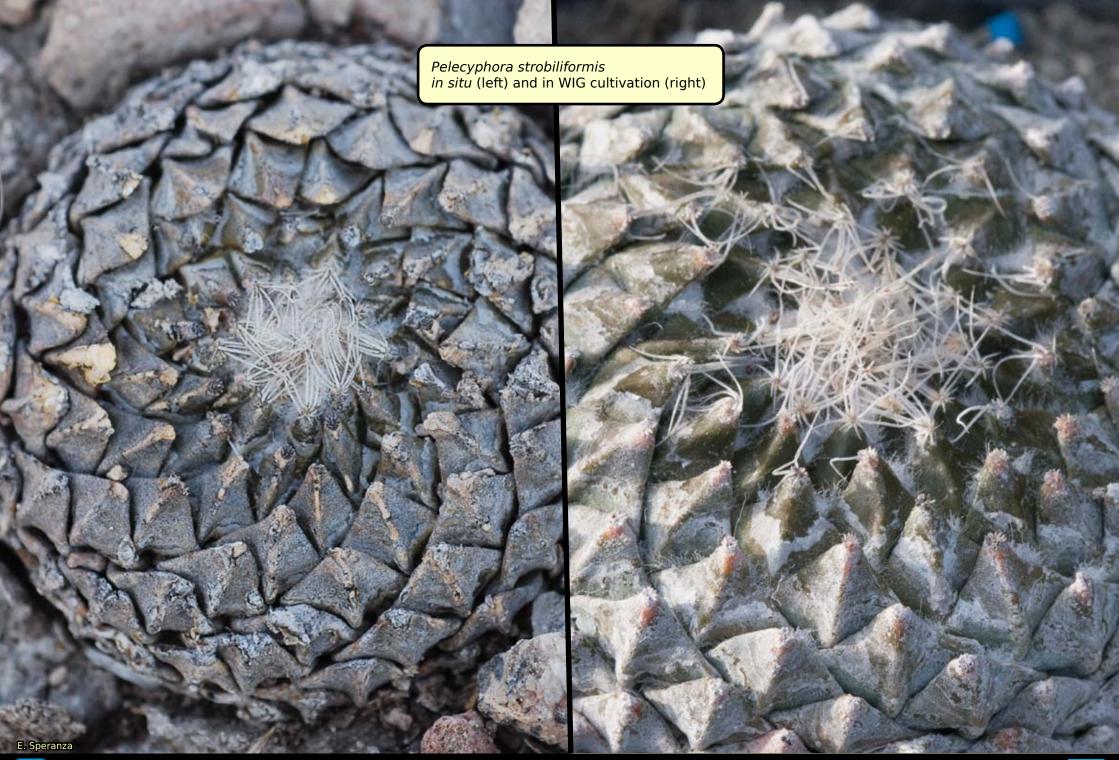
However, the WIG style differentiates from other techniques of extreme cultivation both by the use of mineral substrates similar to natural ones, and by growing plants arranged as they are set up in the wild (e.g. *Aztekium* grown on gypsum in a vertical position).

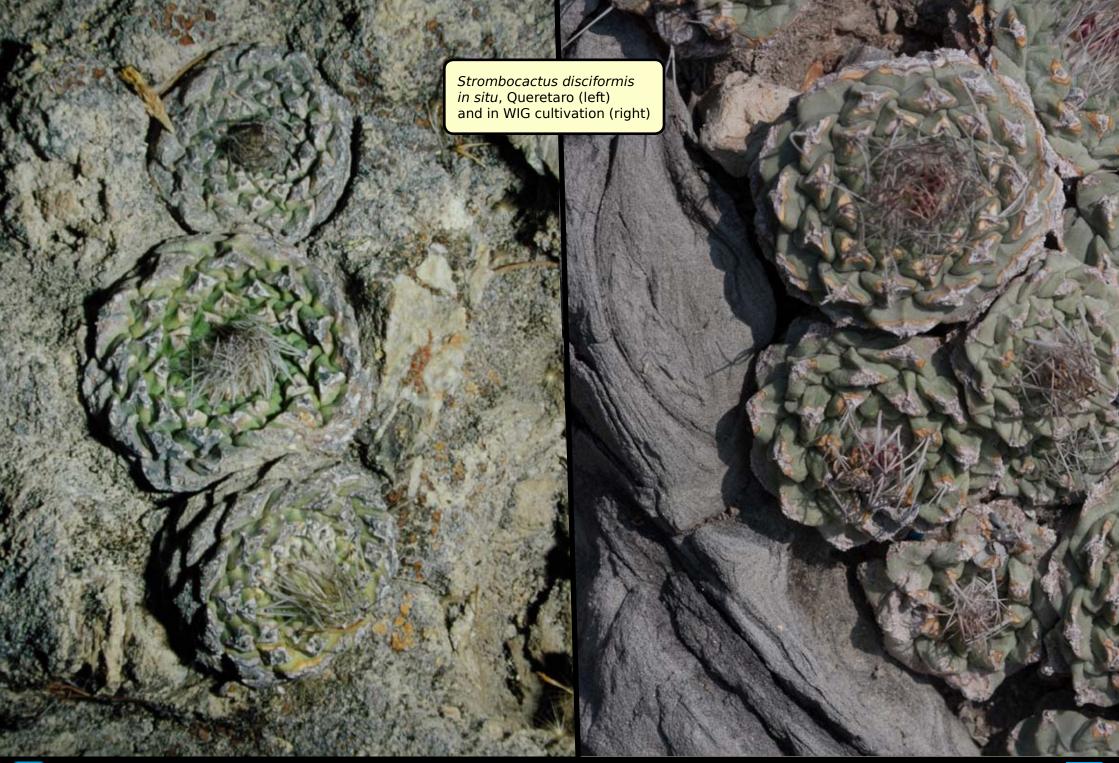
Rules of WIG cultivation

The techniques employed in the style WIG consist in the following:

- Use of natural substrates of proper texture and structure
- Application of a specific fertilization plan
- Providing a suitable solar exposition
- Maximizing the daily thermal variation
- Natural setting up









WIG substrates

The choice to obtain the most suitable substrate for the WIG cultivation was geared primarily to the total elimination of the organic component, namely the peat, which exerts excessive continuous nourishing and moisturizing. Then it was directed to the adoption of mineral compounds with a structure and texture similar to natural soils.

All efforts were spent to obtain a substrate suitable to the cultivation of plants from areas of the Mexican plateau that are characterized by a very slow growth (e.g. plants of the genus Ariocarpus), for which was adopted a soil consisting mainly of marlstone. It is a rock of terrigenous sedimentary nature, widely used in the production of cement, and contains clay which has high cation exchange capacity, conducive to good plant nutrition.

Fertilization plan

Nitrogen in plant nutrition plays a vital role in the formation of the soft tissues (i.e. an excess increases the production of hydrated tissue), but its deficiency can cause disturbances in growth, especially if it is determined in the early stages of development. For this reason, in the WIG style is used a balanced fertilizer (N:P:K = 12:12:12) with the first spring watering in order to boost the activation of growth, then move on to use a low-nitrogen fertilizer (N:P:K = 4:8:16) for the remainder of the year.



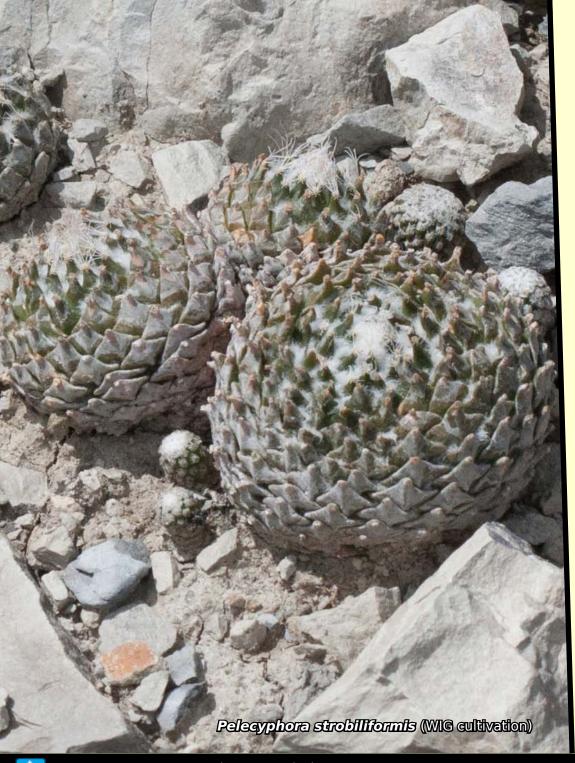
Irradiation

Much of the dry substance which constitutes a plant, such as wood and cellulose derives more or less directly by photosynthesis, whereby a lack of light is reflected immediately in the production of weak spines. Grown in too much shade a plant tries to capture the most available light possible, thus reducing the thickness of the cuticle and stretching it more and more. This phenomenon is called 'etiolation' and should definitely be countered by placing the plants in conditions

of direct sunlight throughout the day. In winter, when the plants are in the greenhouse, direct light can be very weak or absent. In these conditions the arrest of the metabolic functions of the plant should be encouraged as much as possible by keeping the temperature close to zero, so that the plants do not consume the sugars that are stored in tissues during the summer.



It's not only intensity, but also the quality of light that is important. Glass and polycarbonate stops ultraviolet rays and reflects a conspicuous part of useful radiation. Also polythene covers stops ultra-violet rays but may result in better transparency to PAR (photosynthetic active radiations). In all cases, direct sunlight is the better choice for the WIG style.



Daily thermal variation

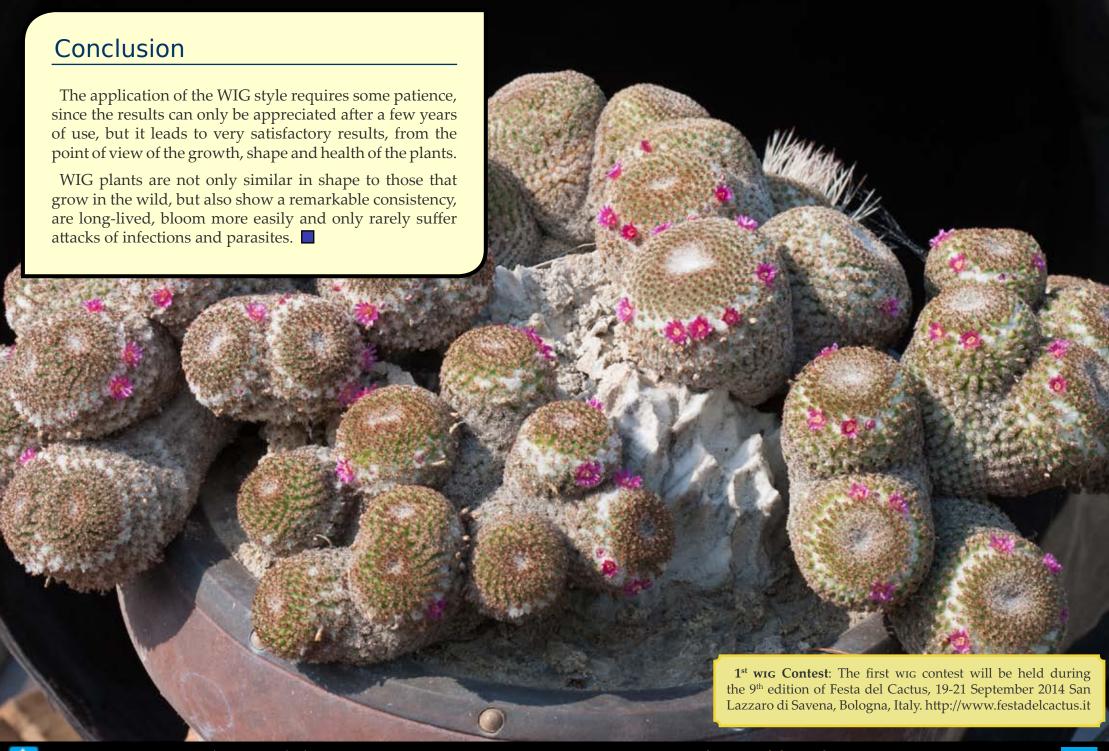
If the greenhouse temperature is high during the night, the plants maintain a high metabolism that consumes part of the sugar produced by photosynthesis during the day, which should be used for the production of spines instead. The WIG style therefore expects us to expose plants to the open-air as much as possible in order to maximize the daily thermal variation.

Irrigation

The natural mineral substrate structure consists of coarse rock fragments with sharp edges and in a thin component essentially made of clay, silt and, sometimes, sand. This constitution determines its quick-drying ability, especially if the cultivation is carried out in the open air. It follows that WIG plants should be subject to frequent irrigations during the period, i.e. whenever the substrate dries. In hotter summer days this can lead to two watering per week. With the approach of the winter season watering must be less frequent, to be ceased entirely by September 15 to stop any further growth.

Natural setting up

For several species placing the plants in their environment strictly depends on ecological factors affecting such species diffusion, e.g. *Aztekium* (and *Strombocactus*) species are adapted to colonize vertical slopes and don't grow in other environments. The cultivation of these species in a vertical position results in better plant growth.







ouseleeks (genus Sempervivum L.) are known for their predilection to grow at high altitudes Lon the upper slopes and summit areas of the mountains in the temperate zone, where the weather still reminds them of the time of glaciations, withstanding intense cold and snow without any problem for months every year. While this reputation is a bit overrated for some species growing at medium or low altitudes, it is perfectly justified for the one we are presenting today: Sempervivum montanum L., a houseleek that struggles to survive below 1,500 m or rather enjoys his life only above 2000 m. A beautiful houseleek, very common and widely distributed in the European mountains but which doesn't allow itself to be easily admired because it won't go down to meet you, you will have to climb up to contemplate it!



Description

Tuft: compact to very compact, medium to well crowded; stolons are usually short (daughter-rosettes are tight against the mother-rosette), rather thin, of variable persistence according to the forms, bearing small leaves spaced and not just papery bracts [stolons may lengthen a lot in cultivation in plain].

Adult rosette: more or less open according to the forms, diam. (1-)2-3(8) cm; few leaves arranged regularly, the anisophylly is usually little or no marked; no stolon is produced during the year of flowering of the rosette but the monocarpy is not always accompanied by the death of the whole stock of the rosette: the base thereof sometimes stays alive (but leafless) at the level where the stolons sprout out after the death of the flower stem.

Leaf: few to highly succulent; apex often blunt, without apicule; often quite dark green sometimes tinged with greyish, absent or reddish slightly marked and diffuse apical spot; fully and densely glandular-hairy, sticky, musky more or less intense smelling but often very strong and recognizable; marginal cilia rather poorly differentiated from facial hairs.

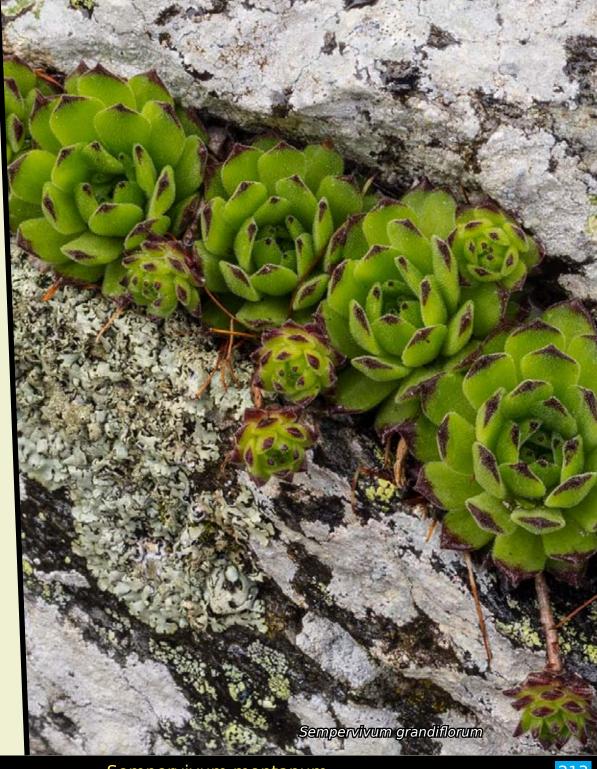
Inflorescence: terminal; carried by a low or moderately high stem (5-25 cm) but most frequently short; sparse inflorescence with rarely more than 5 or 6 flowers blooming at the same time; cauline leaves abundant throughout the height of the stem, quite large and regular size without significant difference in size between lower and upper leaves. The contrast between the large size of the flower and the shortness of the flower stem is very characteristic of this species among houseleeks.

Flower: often quite large relative to the small size of the rosette, but the diameter varies greatly depending on the geographical populations (1.5-)2-3(-3.5) cm; many petals (about 15, but very variable number), long tapering, bright lilac-pink with a purple indistinct longitudinal stripe in the middle of the blade, giving globally a fairly typical vinous rose colour, very rarely duller and shading to whitish but with constantly a purple basal spot; purple filaments. A few rare individual variations with yellow flowers can be found here and there.

Possible confusion

Among European houseleeks, Sempervivum montanum may possibly be confused with Sempervivum grandiflorum Haw. (1) in the vegetative state: especially the non-flowering rosettes of S. montanum subsp. burnatii Wettst. ex Hayek (cf. infra) but these plants are easy to differentiate at flowering time, because the flower of S. montanum is wine red, while that of *S. grandiflorum* is yellow. Confusion between S. montanum and S. grandiflorum is even easier in the case of the rare yellow-flowered variant of *S. montanum*, but the latter being very rare this confusion is unlikely. Rosettes of S. montanum subsp. heterophyllum (Hazsl.) Jáv. ex Soó (cf. infra) have also a quite similar aspect to those of S. grandiflorum, but their respective areas are very distant from each other and thus prevent any confusion.

In practice, the most frequent confusion *in situ* is the confusion of *S. montanum* with one of its many hybrids, particularly with *Sempervivum* × *barbulatum* Schott, which we discuss below. As most of these hybrids are generally fertile, backcrosses of them with *S. montanum* are common, with introgression of characters from one parent species to the other, and the resulting plants are often very difficult to differentiate from *S. montanum* itself, sometimes impossible out of flowering.



Donati D. & Dumont G. (2014), Sempervivum grandiflorum, in *Acta Succulenta* 2(1): 91-108.

A bit of nomenclature

Sempervivum montanum L., Species Plantarum, ed. 1, 1: 465 (1753) [ed. 2, 1: 665 (1762)]

Typus: Lectotypus, Herb. Burser, UPS, 16(1): 55; design. Letz & Marhold in *Taxon* 45: 114 (1996) // Epitypus, WU, leg. Handel-Mazzetti, s.n., 1906-08-08; Engadin, Piz Padella, 2300 m; design. Letz & Marhold in *Taxon* 45: 114 (1996)

Synonymy:

- *Sempervivum tectorum* subsp. *montanum* (L.) Bonnier
- *Sempervivum candollei* Rouy & E.G.Camus
- = Sempervivum flageliforme Fischer ex Link
- = Sempervivum montanum f. flageliforme (Fischer) H.F.R.Miller
- = Sempervivum montanum var. medium DC.
- = Sempervivum hispidulum Schott

Chromosome number: 2n = 42.

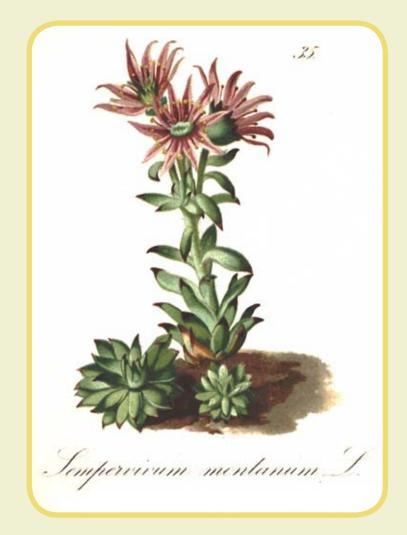
An unnecessary controversy

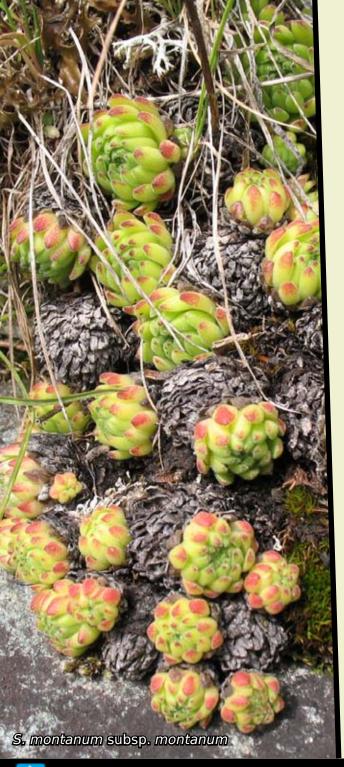
As with all the diagnoses of Linnaeus, that of *Sempervivum montanum* is very short but the problem is that it can easily be applied to several houseleeks from the Alps:

{*Sp. Pl.* ed. 1} SEMPERVIVUM foliis integerrimis, propaginibus patulis. Habitat in rupibus Helvetiae. [perenne]

{Sp. Pl. ed. 2} SEMPERVIVUM foliis ciliatis, propaginibus patulis. Habitat in rupibus Helvetiae. [perenne]

Basing themselves on the impossibility to recognize a precise houseleek from this diagnosis, as well as some apparent contradictions between the plant and its diagnosis (indeed Linnaeus insists on the cilia in *Sp. Pl.* ed. 2, while those are not very obvious in this species compared to those of some other houseleeks) some authors such as Rouy & Camus argued that the original plant of Linnaeus was not the plant usually designated by this name and therefore proposed to rename it (*Sempervivum candollei* Rouy & EGCamus). The fact that they are historically right (which is not certain) does not have to be taken into account because the application of this name since its publication has been widely established by usage and without any ambiguity. Furthermore, this debate is now nomenclaturally closed since the lectotypification of this name in 1996 (see above).





Variability and subordinate taxa

As we have already mentioned, *Sempervivum montanum* is a plant widely distributed in European mountains. The vast extent of its natural area associated with the variability that characterizes all houseleeks make *S. montanum* globally a very variable species, with numerous geographical forms.

However, it should be noted that the populations of *Sempervivum montanum*, if considered locally and separately, are generally fairly homogeneous compared to those of some other houseleeks, if we don't take into account of course the presence of its hybrids (direct hybrids and possible backcrosses), which can be very numerous.

This relative homogeneity of the local populations of *Sempervivum montanum* associated with the high variability of this species considered at the level of its overall area, has lead to the fact that many of these geographic forms have been described taxonomically in the past, but their nomenclatural value is more than questionable, and at best very low, and they can therefore mostly be reversed into the type-species, unless you agree to describe two or three new taxa for each mountain...

Based on ecological, physiological, morphological and secondarily geographical criteria, there can be recognized in this species, considered in its broadest sense, four main types, to which it seems convenient and relevant to afford the rank of subspecies for three of them:

- Sempervivum montanum subsp. montanum
- Sempervivum montanum subsp. burnatii
- Sempervivum montanum subsp. heterophyllum
- (Sempervivum montanum subsp. stiriacum)

The fourth type (*stiriacum*), although usually considered at the rank of sub-species of *Sempervivum montanum*, deserves, due to its characteristics, a separate treatment (cf. infra).

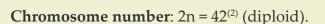
Within these broad taxonomic frameworks, it would be of course possible to individualize a few varieties and forms, whose justification may sometimes be argued but whose interest is by far more anecdotal. As always, the problem with houseleeks is not to recognize and individualize the local microforms (that would be endless and totally useless) but to recognize and define the major taxonomic frameworks for these highly variable plants with strongly hybridized populations. Indeed, it is always easier to recognize what differentiates from what unites...

Sempervivum montanum subsp. montanum

(autonym)

Synonymy:

- *≡ Sempervivum montanum* var. *montanum* auct.
- = Sempervivum montanum subsp. carpaticum Wettst. ex Hayek
 - *Sempervivum carpathicum* Wettst. ex Prodan
 - *≡ Sempervivum montanum* subsp. *eumontanum* var. *carpathicum* (Wettst.) Domin
 - *≡ Sempervivum montanum* var. *carpaticum* (Wettst.) Praeger
 - *≡ Sempervivum wettsteinii* Letz
 - = Sempervivum montanum f. brachypetalum Domin
 - = Sempervivum montanum f. congestum Domin
 - = Sempervivum montanum f. speciosum Domin
 - = Sempervivum montanum f. stenophyllum Domin
- = Sempervivum montanum var. ochroleucum Beauverd
 - *≡ Sempervivum montanum* f. *ochroleucum* (Beauverd) Ingw.
- = Sempervivum montanum var. pallidum Wettst. ex Hayek
 - *≡ Sempervivum montanum* f. *pallidum* Schinz & Keller
 - *≡ ?Sempervivum montanum f. pallidum (Wettst. ex Hayek) sensu Domin*
- = *Sempervivum alpestre* Lamotte
 - *Sempervivum candollei* [var.] *alpestre* (Lamotte) Rouy & E.G.Camus
- = *Sempervivum debile* Schott
 - *≡ Sempervivum montanum* subsp. *debile* (Schott) Dostal
 - ≡ Sempervivum montanum subsp. eumontanum var. debile (Shott) Domin
 - *Sempervivum montanum* var. *debile* (Schott) Chenevard
- = *Sempervivum macranthum* Jeanb. & Timb.-Lagr.
 - *Sempervivum montanum* [var.] *macranthum* (Jeanb. & Timb.-Lagr.) De la Soie
- = Sempervivum minimum Timb.-Lagr.
 - ≡ Sempervivum montanum var. minimum (Timb.-Lagr.) H.Huber ex H.Jacobsen
 - *Sempervivum montanum* subsp. *minimum* Huber ex Köhlein
 - *≡ Sempervivum tectorum* var. *minimum* (Timb.-Lagr.) Bonnier





- = Sempervivum minimum [var.] baregense Rouy
- = Sempervivum monticolum Lamotte
 - *≡ Sempervivum montanum* var. *monticolum* (Lamotte) H.Jacobsen
 - $\equiv Sempervivum \ montanum \ subsp. \ monticolum \ (Lamotte)$ ex Köhlein
- = Sempervivum pygmaeum Jeanb. & Timb.-Lagr. (non C.Sm. ex Link)
 - *Sempervivum montanum* var. *pygmaeum* (Jeanb. & Timb.-Lagr.) Lagger ex Conill & Despaty
- $= Sempervivum \ subalpinum \ {\bf Rouy}$
 - $\equiv Sempervivum\ candollei\ [var.]\ subalpinum\ (Rouy)\ Rouy\ \&\ E.G. Camus$
 - *≡ Sempervivum montanum* var. *subalpinum* (Rouy) Beauverd
- = Sempervivum submontanum Rouy ex H.Jacobsen
- = Sempervivum bambergii Hamp. ex Lagger
- = Sempervivum thomasii Lagger

Sempervivum montanum subsp. montanum is a plant with quite small to medium rather closed rosette, with a more or less globular and compact habit, more or less dark green, sometimes taking a frosted appearance because of glandular secretions, with lanceolate or more or less linear leaves.

Zésiger F. (1961), Recherches cytotaxonomiques sur les Joubarbes, Note préliminaire, in Ber. Schweiz. Bot. Ges. 71: 113-117.

The populations of Sempervivum montanum subsp. montanum corresponds to the populations of the central Alps, a large part of the western Alps, the Pyrenees and the northern Carpathians, i.e. the vast majority of the populations of the species. In these areas, it is a typical plant of the crystalline regions of the upper mountain belt and of the subalpine and alpine belts, where it is extremely frequent.





About the subsp. *carpaticum*:

The Carpathian plants from high altitudes, long considered as a subspecies of its own and named Sempervivum montanum subsp. carpaticum Wettst. ex Hayek(3) [in Hegi, Illustrierte Flora von MittelEuropa, ed. 1, vol. 4(2): 554 (1923)] should, in our opinion, be regarded as nothing more than one of the many geographic forms of subsp. montanum, which is a plant morphologically very variable, and therefore reversed therein.

Subsp. carpaticum is a plant that has, in the area where it is individualized at its best (Western Carpathians: Mounts Tatra and neighbouring ranges), slightly apiculate leaves of a pretty light green; this individualization from the type montanum is quite minor and easily integrates into the usual range of variability of subspecies montanum; moreover the morphology of the populations of "subsp. carpaticum" of the north-eastern Carpathians (in Ukraine and Romania) rather tends toward the type montanum with little specificity with respect to the Alpine type.

The individualization of the subsp. carpaticum from the type montanum is therefore, in our opinion, too vague and too low and the morphological continuum with it is too obvious to give it a real subspecific status. Its individualization is essentially and almost only geographical; in addition its ecology is not different from that of subsp. montanum. Also note that the consideration of this taxon, regardless of rank that it grants, would lead, for reasons of coherency of the infraspecific nomenclature of S. montanum, to take into account many other "taxa" in this species whose nomenclature then would explode uselessly and without relation to the reality of this basically very variable species. Note that the multiple taxa, which would then be taken into account, would not be all simple local forms but sometimes large geographic populations such as the Pyrenean populations. This explosion of the nomenclature of *S. montanum* on macro and micro-geographical basis is a possibility but it is not our view and we consider here the subsp. carpaticum as a simple synonym of subsp. montanum.

The usual attribution of this name to Wettstein is in fact only assimilation: indeed, Hayek attributes to this author the other names of sub-species of Sempervivum montanum, and only the latter remains unassigned; it is therefore a probable typographical oblivion. Note that Wettstein is cited in notes as a collaborator of Hayek, the latter being the author of the Sempervivum part in the Flora of Hegi. Moreover, the explicit reference of this epithet to Wettstein exists in Prodan 1923.





Sempervivum montanum subsp. burnatii Wettst. ex Hayek

Sempervivum montanum subsp. burnatii Wettst. ex Hayek, in Hegi G., Illustrierte Flora von MittelEuropa, ed. 1, vol. 4(2): 554 (1923)

Synonymy:

- ≡ [Basionyme] *Sempervivum burnatii* Wettst. ex Burnat
- *Sempervivum montanum* var. *burnatii* (Wettst.) Praeger
- = Sempervivum montanum subsp. burnatii f. maximum Gamisans
- = Sempervivum frigidum Lamotte
 - *Sempervivum montanum* subsp. *frigidum* (Lamotte) Marcailhou
 - *≡ Sempervivum montanum* var. *frigidum* (Lamotte) Chas

Chromosome number: $2n = 42^{(4)}$ (diploid).

Sempervivum montanum subsp. burnatii is well differentiated from subsp. montanum by:

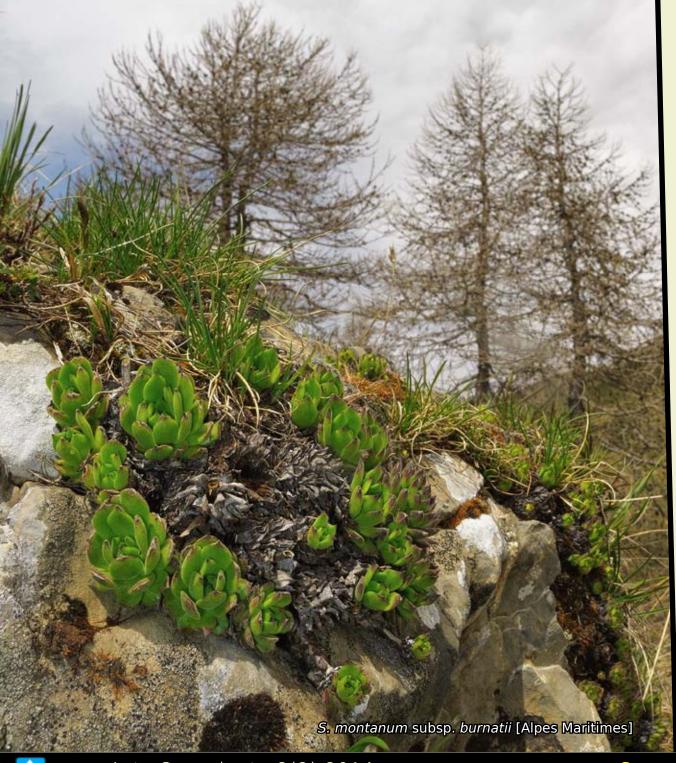
- <u>Its morphology</u>: its bigger overall size, its more open rosettes, its much broader, sometimes very broad, and often markedly spatulate leaves (maximum width at the distal half and not as at the proximal half as in subsp. *montanum*), which are very glandular and fragrant, its large flowers.
- <u>Its physiology</u>: flowering is slightly earlier than that of the subsp. *montanum*⁽⁵⁾ of about ten days to two weeks.
- <u>Its ecology</u>: its ecological latitude is greater than that of subsp. *montanum*, allowing it to colonize a wider variety of locations. It is indeed one the rare houseleeks that you can encounter on vertical rocks facing south (true solar ovens in summer) as well as in full shade in the undergrowth of conifers. It is indeed not uncommon in high larch forests where it can form pretty large mats, sometimes down to lower part of the mountain belt. These conifers lose their leaves in winter and the winter brightness of these stations is high, the summer brightness is higher than in pine or spruce forests but it is still very attenuated and the other houseleeks cannot settle there permanently. Note that the northern boundary of subsp. *burnatii* matches that of the larch forests, i.e. at the level where this ecological advantage disappears. Its lower limit in altitude is also somewhat lower than that of subsp. *montanum*, it is able to go lower down much more obviously in the mountain belt⁽⁶⁾ than the latter.

Because of differences in latitude, it is more rigorous to think in vegetation levels rather than in altitude, vegetation levels going up when the latitude decreases. Two plants growing in the same physical altitude but at different latitudes actually grow in different ecological altitudes.



Zésiger F. (1961), Recherches cytotaxonomiques sur les Joubarbes, Note préliminaire, in *Ber. Schweiz. Bot. Ges.* 71: 113-117.

This is not always easy to verify *in situ* because of variations in flowering time related to latitude and altitude but becomes very obvious by placing individuals of both subspecies into uniform cultivation.



When *Sempervivum montanum* subsp. *burnatii* is morphologically well characterized (because, as all houseleeks, it is also quite variable), it is plainly recognizable at first glance, not only *in situ* but also in cultivation in the plains, despite the morphological deformation that it undergoes like all the other *S. montanum* (considerable lengthening of stolons and stems).

Sempervivummontanumsubsp.burnatiicorresponds to the populations of the southwestern crystalline Alps (Dauphiné, Maritime Alps), Corsica and the Tosco-Emilian Apennine.

Phylogenetic hypotheses:

Sempervivum montanum subsp. burnatii is probably a houseleek of ancient origin in the genus Sempervivum, as evidenced by its presence in both Corsica and the mainland. In Corsica, it is the only form of *S. montanum* that is present and it is accompanied there by one other species of houseleek, Sempervivum arachnoideum L. It is important to note that Sempervivum tectorum L. is absent⁽⁷⁾ in Corsica while it is present in *all* the massifs surrounding Corsica (Pyrenees, Massif Central, Alps, Apennines) where it regularly accompanies S. montanum or is nearby, forming with the latter and with S. arachnoideum a characteristic "trio" of these massifs (Nb: this "trio" is incomplete in the French Massif Central because of the too low altitude for *S. montanum*).

⁷ S. tectorum is present there only as an escapee from cultivation. This species is probably of post-glacial origin, therefore more recent, and we have already presented its probable phylogeny in Donati D. & Dumont G. (2013), Sempervivum soculense, in Acta Succulenta 1(2): 116-146.

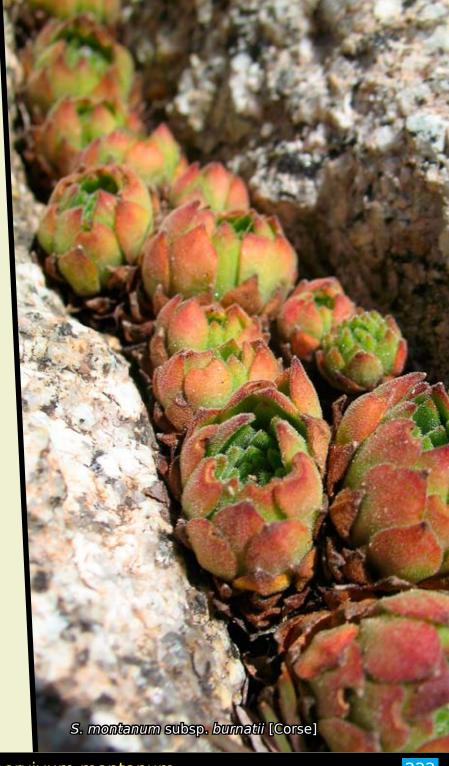
Corsica began to separate from the continent during the Tertiary Period (during the Oligo-Miocene, about 22 to 30 million years BP) and the separation is complete for about 6-7 million years BP apart from a brief and rather hypothetical episode at the heart of glaciation (the Tyrrhenian bridge⁽⁸⁾). The presence of *S. montanum* subsp. *burnatii* both in Corsica and the mainland thus demonstrates that this plant (or more precisely its ancestral form) already existed locally during this separation because a secondary implantation from the mainland to Corsica or the reverse would be difficult to explain. If we even assume that the colonisation is secondary from the mainland, it is extremely old, via the hypothetical Tyrrhenian bridge during glaciations, but this hypothesis is doubly doubtful: doubtful for the effective existence of the Tyrrhenian bridge, and doubtful because it was very hard for plants adapted to high altitude to exploit it, even during glaciations.

Later, during glaciations, the populations of this plant inhabiting the Southern Alps were probably pushed southwards by the glaciers to lower elevations in non-glaciated shelter-areas of the siliceous regions of the Maritime Alps and of the Tosco-Emilian Apennines. Concerning the populations of this plant in Corsica, they have been little affected by glacial phenomena.

During post-glacial warming, plants of the Tosco-Emilian Apennines remained isolated on the high summits of this sandstone massif, which is surrounded by limestone mountains, not allowing a large post-glacial expansion of this acidophilous plant. Today we can see that the morphology of the plants of the Apennines is very close to that of the Corsican plants.

Very interesting are the populations of subsp. *burnatii* which today inhabit the siliceous areas of Dauphiné and the Maritime Alps, because they are morphologically differentiated from the plants of Corsica and of the Apennines: their leaves are very broad and very spatulate, obtuse, almost truncated. This differentiation does not justify individualising them taxonomically but it is important to note it because it demonstrates that the recolonization of the Southern Alps was accompanied by a more important evolutive exacerbation than in Corsica or Apennines, probably due to the differences of selective pressure between their shelter-areas and the areas of postglacial recolonization (remember that this phenomenon of recolonization was little or un-marked for plants of Corsica and Apennines).

During the strongest of glaciations, the lowering of the sea level in the Tyrrhenian basin would have temporarily connected Corsica to the current Tuscany by the so-called "Tyrrhenian bridge", which, it seems, remains a geological hypothesis that is not rigorously proven.





Relationship with the subsp. montanum:

The presence of this subspecies in Corsica <u>and</u> the mainland while the subsp. <u>montanum</u> is present <u>only</u> on the continent would lead one to think that subsp. <u>burnatii</u> is closer to the ancestral type of the species than subsp. <u>montanum</u>, which would be a derived type. This is however a hypothesis.

In the north-western Alps, subsp. *burnatii* meets subsp. *montanum* and there are many intermediate individuals. This apparent *continuum* could lead to refute the subspecific status of the type *burnatii*. It would be a mistake, because if we look closer, we see that the composition of the contact area is more an entanglement of these two types of plants than a pure morphologic *continuum*. Entanglement of two subspecies of the same species is nevertheless an unusual fact allowing one to refute the distinction between these subspecies. In fact, two important physiological and ecological factors mentioned above, allow, in this case, explaining of such entanglement:

- 1. Flowering of subsp. *burnatii* is earlier than that of subsp. *montanum*, which is a factor of genetic isolation and allows locally the parallel maintenance of two lineages. However, some overlap exists and this isolation is not complete which allows some crosses and therefore maintains a somewhat morphological *continuum* between the two parent lineages.
- 2. Subsp. burnatii can colonize sites such as larch forests (covering considerable areas in the Southern Alps) that subsp. montanum cannot do. This allows maintaining the characteristics of subsp. burnatii even if subsp. montanum is present not far away. Note that the narrowing of the ecological flexibility of a form assumed to be derived (subsp. montanum) in relation to the form from which it derives (subsp. burnatii if our hypothesis is followed) is not an exceptional phenomenon. In this case, there has been a specialization of the plant for open environments in altitude. Note in this regard that subsp. burnatii is absent from the core of the Alps, the area of the highest massifs, where subsp. montanum abounds by contrast.

All the above leads us to consider the rank of subspecies for this taxon as relevant and justified.

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Sempervivum montanum subsp. heterophyllum (Hazsl.) Jáv. ex Soó

Sempervivum montanum subsp. heterophyllum (Hazsl.) Jáv. ex Soó in Vergleichende Vegetationsstudien, Zentralalpen, Karpathen, Ungarn, nebst kritischen Bemerkungen zur Flora der Westkarpathen, in Veröff. Geobot. Inst. ETH Stiftung Rübel, Zürich, 6: 246 (1930)

Synonymy:

- **=** [Basionym] *Sempervivum montanum* [var.] *heterophyllum* Hazsl.
- *≡ Sempervivum heterophyllum* Hazsl. ex Dostal
- *≡Sempervivum carpathicum* subsp. *heterophyllum* (Hazsl.) Letz
- *≡ Sempervivum wettsteinii* subsp. *heterophyllum* (Hazsl.) Letz
- = Sempervivum montanum f. majus Domin

Chromosome number: $2n = 42^{(9)}$ (diploid).

Sempervivum montanum subsp. heterophyllum is a subspecies of S. montanum which, although anciently known, has long been neglected although it appears clearly differentiated from the other subspecies.

Sempervivum montanum subsp. heterophyllum is a native of the Western Carpathians, more precisely the southern Carpathian foothills (in central Slovakia). Its area therefore is not confused with that of subsp. *montanum* (syn. subsp. *carpaticum*) that grows on the high summits of the Carpathian main range further north (Mount Tatra and neighbouring Carpathian ranges).

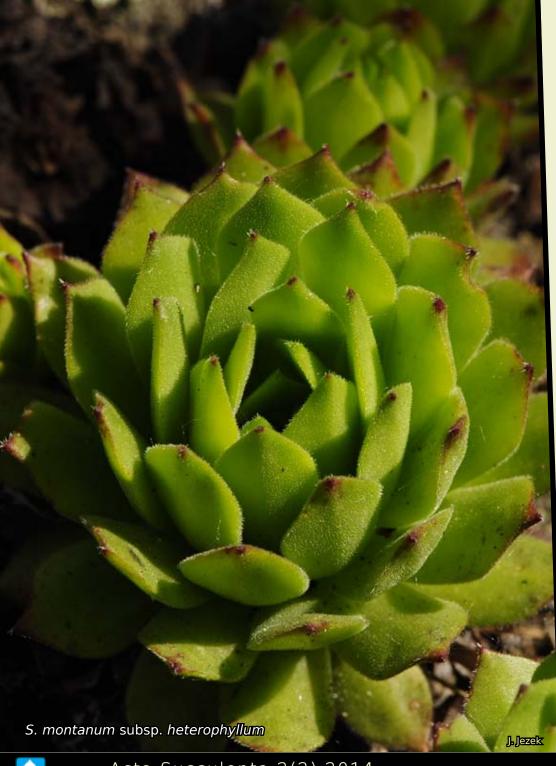
Morphologically, subsp. heterophyllum has very large rosettes for Sempervivum montanum, 4-7 cm in diameter and rather open, with relatively persistent stolons and rather pale green leaves, which are few, broad and spatulate but hardly succulent.

A surprising houseleek:

What is most remarkable from an ecological point of view is that this subspecies is indeed a plant of very low altitudes, its populations growing at less than 1,000 m (from 260 m) which is exceptional for a Sempervivum montanum, all the other forms of this species being plants from altitudes and even from very high altitudes.

Boscaiu M. in Letz R. & al. (1999), Chromosome numbers of several interesting taxa of the flora of Slovakia, in *Biologia*, Bratislava, 54(1): 43-49





Sempervivum montanum subsp. heterophyllum colonizes the sites of silicate effusive rocks in this primarily limestone region, because like all the other Sempervivum montanum, this plant is strictly acidophilous. The locations where this plant grows are often rocky islets, sometimes even simple rock walls, emerging from the forests that cover (or formerly covered) this region. This plant is considered as rare, but because of its habitat spread in small and localized populations, the numbers of the overall population are likely to be underestimated.

Phylogenetic hypotheses:

The habitat of *Sempervivum montanum* subsp. *heterophyllum* strongly suggests a plant in a situation of post-glacial relict, which it probably is. Its ancestors probably found refuge in the southern Carpathian foothills during Quaternary glaciations, after being pushed down to these low altitudes by glaciers.

During the post-glacial warming, these plants have stayed there, isolated on islets of silicate rocks by the rapid development of forests; their gradual adaptation to the conditions of the lower altitudes was probably facilitated by the continental climate with long and relatively cold winters of this region.

If one considers this plant as a relict, it is possible that it kept a state fairly close to the ancestral state of *S. montanum*, at least for some of its characters. We have mentioned above that the subsp. *burnatii* is probably also relatively close to the ancestral state of *S. montanum* during Tertiary times, particularly its populations of Corsica and the Tosco-Emilian Apennines. Comparing the morphology of these two geographically distant subspecies further strengthens this hypothesis and thus leads to assume that *S. montanum*, as we know it today, is derived from an ancestral pre-glacial population of houseleeks with large rosettes and broad flat hairy leaves and that global population already colonized the Alps and the Carpathians during the Tertiary period.



The question of Sempervivum stiriacum

In the Eastern Alps, from the Großglockner massif and in all the remaining ranges eastwards from this massif, *Sempervivum montanum* subsp. *montanum* is replaced by a taxon that is generally regarded as one of its subspecies: *Sempervivum montanum* subsp. *stiriacum* Wettst. ex Hayek.

A seemingly simple problem...

This plant is usually considered as a vicarious⁽¹⁰⁾ subspecies of subsp. *montanum* in the Eastern Alps. It shows a relative morphological individualization: rosettes of similar size or slightly bigger (2-4 cm diam.) than those of *S. montanum* subsp. *montanum* with slightly more leaves, which are sometimes narrower but often flatter and more tapering, more acute, with a dark apical spot which is well marked and *without gradient*, which is an unusual feature for a *S. montanum*. Karyologically, this plant is tetraploid (2n = 84). It would be the only known tetraploid (2n = 42). Ecologically, it is a silicicolous plant as are all *Sempervivum montanum* (the few occurrences of it in limestone regions corresponds to crystalline islets in limestone areas), but it goes a little lower down in elevation than the subsp. *montanum*.

... which proves to be more complicated than it seems

If we limit ourselves to the foregoing, this taxon *stiriacum* appears indeed to be only a well individualized tetraploid form of *S. montanum*, for which the status of subspecies would therefore seem imperative. However, its field study shows that this conclusion is probably hasty:

The taxon B is vicarious of the taxon A if A and B are related but differentiated, and occupy the same ecological niche but in two independent but not directly adjacent territories.





- The type *stiriacum* replaces the type *montanum* in the Eastern Alps and the two forms come into contact in the central Alps, but in this contact zone, there are no hybrid or intermediate forms between them. This demonstrates the difficulty of crosses⁽¹¹⁾ between these two plants; this fact is very rare in the genus *Sempervivum*, even between different species.
- These two forms are present together in the seam zone of the Großglockner massif where they occupy very close but *different* sites, with a clear *vertical zonation*, the subsp. *montanum* growing above the "subsp. *stiriacum*" apparently *without any mixed population*. This shows a clear difference in their ecological requirements, so we cannot speak of simple vicariance.
- The coexistence in the same zone of two different subspecies of the same plant species is a rather unusual phenomenon, and in such a case, an entanglement or a *continuum* would be noticed (see above the remarks about subsp. *burnatii*). This is impossible to detect in the case of these two plants, the recognition of one or the other plant in their zone of contact is without problem and the micro-populations are homogeneous, corresponding to one or the other plant and topographically well separated.

If we add to these field data the characters mentioned above:

- -A morphological differentiation which is easily recognizable.
- -A karyological differentiation (tetraploid).

We consider it unreasonable to speak in this case of two subspecies of a single species, and we believe it is justified to consider this taxon with a specific rank, this opinion being based on morphological, chorologic, ecological and karyological arguments. Note that this taxon was rightly described initially as a species:

¹¹ Their hybrid would be triploid, therefore probably not very fertile. This would explain the absence of backcrossing but not the absence of direct hybrids.

Sempervivum stiriacum Wettst. ex Hayek in *Flora von Steiermark* 1: 688 (1909)

Synonymy:

- *Sempervivum montanum* subsp. *stiriacum* Wettst. ex Hayek
- *Sempervivum montanum* var. *stiriacum* (Wettst.) Praeger
- *Sempervivum braunii* Funk ex W.D.J.Koch
 - = Sempervivum montanum var. braunii (Funk) Wettst. ex Hayek
 - = Sempervivum stiriacum [var.] braunii Wettst. ex Hayek
 - = Sempervivum montanum f. braunii (Funk) Guillaumin

Chromosome number: $2n = 84^{(12)}$ (tetraploid).

NB: Sempervivum braunii Funk ex W.D.J.Koch is only a variant with yellowish flowers rarely encountered here and there, to which it would not be reasonable to grant a nomenclatural status.

A very precise and very particular area

Sempervivum montanum s.s. is now totally absent from the Eastern Alps. It is however omnipresent in the western and central Alps. The Großglockner massif represents its eastern limit in the Alps range.

Similarly, *Sempervivum stiriacum* is present and common in the Eastern Alps, but is totally absent further west, in the central and western Alps. Eastward, in the nearby Carpathians, *S. stiriacum* is totally absent and one finds again the diploid *S. montanum*, as in the Western Alps.

The overall area of *S. montanum* in the Alps and the Carpathians is brutally interrupted in the Eastern Alps, where it is fully substituted by *S. stiriacum* which establishes a sort of bridge between the eastern and western populations of *S. montanum* (from that comes the fact that it was considered as a simple local vicarious, we have shown above that this is not exactly the case).



In this old engraving from the eighteenth century representing "S. montanum" and dated before the description of S. stiriacum, we can easily recognize the latter.

[Jacquin, N.J. von, Florae austriacae, 5: tab. 41 (1778)]



² Zésiger F. (1961), Recherches cytotaxonomiques sur les Joubarbes, Note préliminaire, in *Ber. Schweiz. Bot. Ges.* 71: 113-117.

Phylogenetic hypotheses

While considering Sempervivum stiriacum at the specific rank, we do not deny the close relationship between these two species: their appearance is rather close, their flowers are the same and they are both strictly silicicolous. S. stiriacum is obviously a tetraploid species derived from S. montanum, or at least from its ancestors, appeared by doubling of the chromosome stock of the latter $(42 \times 2 = 84)$. Indeed, an autotetraploid form always derives from a diploid and not the reverse. We can thus say with little risk of error that *S. stiriacum* appeared in the Eastern Alps secondarily from the diploid *S. montanum* but this appearance is probably old; the two branches have then evolved independently and today S. stiriacum is no longer just a tetraploid S. montanum (cf. supra).

It is likely that *S. stiriacum* has gradually and now completely replaced *S. montanum* in the Eastern Alps. The best adaptation of *S. stiriacum* to moderate altitudes that characterize this part of the Alps has certainly contributed to this supplantation of competitive nature. Besides, when *S. stiriacum* is present, *S. montanum* succeeds to locally persist only when the altitudes rise sufficiently for it to grow over *S. stiriacum* without direct competition, this is the case in the Großglockner massif which is the current confrontation area of these two taxa.





A very competitive tetraploid plant

Polyploidy is known to often increase vigour and adaptation capacity of the organism concerned (due to the increase of the number of genes and homologous alleles) and thus make it more competitive in comparison with diploids from which it derives, but this is verified only for allopolyploids (i.e. additives crosses between different species) and not for autotetraploids (simple doubling of the chromosome stock of a diploid species). Indeed, an autopolyploid is often the victim of the expression of recessive defects and its fertility is often lower⁽¹³⁾ than that of the diploid from which it derives. One observes generally that an allopolyploid can easily supplant one of the diploid from which it derives, while an autotetraploid will tend to coexist with the original diploid as simple "chromosomal race" present here and there but it will not tend to supplant it, especially not totally as is the case here.

In the case of *Sempervivum stiriacum*, increased adaptability is proven by the fact that this plant adapts to lower altitudes and more varied habitats than *S. montanum* and increased competitiveness is demonstrated by full supplantation of *S. montanum* throughout the large area where *S. stiriacum* is present.

How to explain that?

Sempervivum stiriacum is either an unusual autotetraploid regarding its competitiveness, but in the field of life what is unusual is never impossible, or it is not a real autotetraploid but an allotetraploid coming from the additive cross of S. montanum with another houseleek from the Eastern Alps, today disappeared and totally supplanted by the tetraploid. This houseleek therefore had a chromosome number of 2n = 42, like S. montanum, or slightly higher because some chromosome pairs are sometimes lost during the process of polyploidization. This plant has, apparently, left no trace, so this hypothesis is highly speculative but nevertheless cannot be totally dismissed.

The not improbable hypothesis that *Sempervivum stiriacum* is a disregarded allotetraploid, whose only one parent is *S. montanum*, would of course strengthen the point of view consisting to consider it as a species of its own and not merely as subspecies of *S. montanum*.

Reduced fertility due to meiotic anomalies related to the formation of tetravalents instead of bivalents.



Ecology

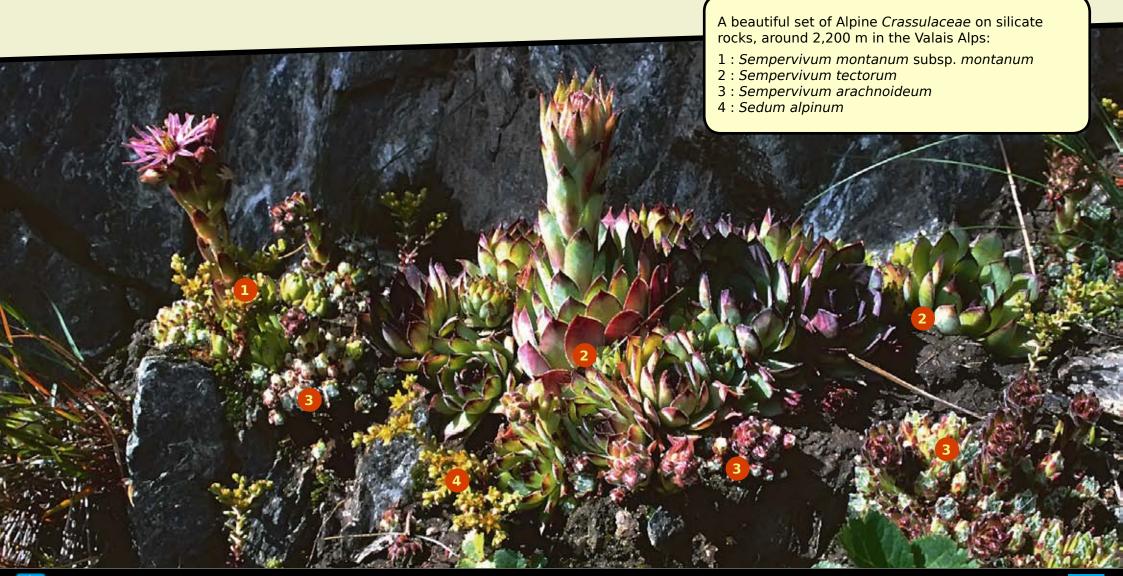
Sempervivum montanum is a plant of high altitudes (except its subsp. heterophyllum), with a behaviour not really psychrophilous but at least needing high nycthemeral temperature ranges with what seems the most important parameter: cold nights.

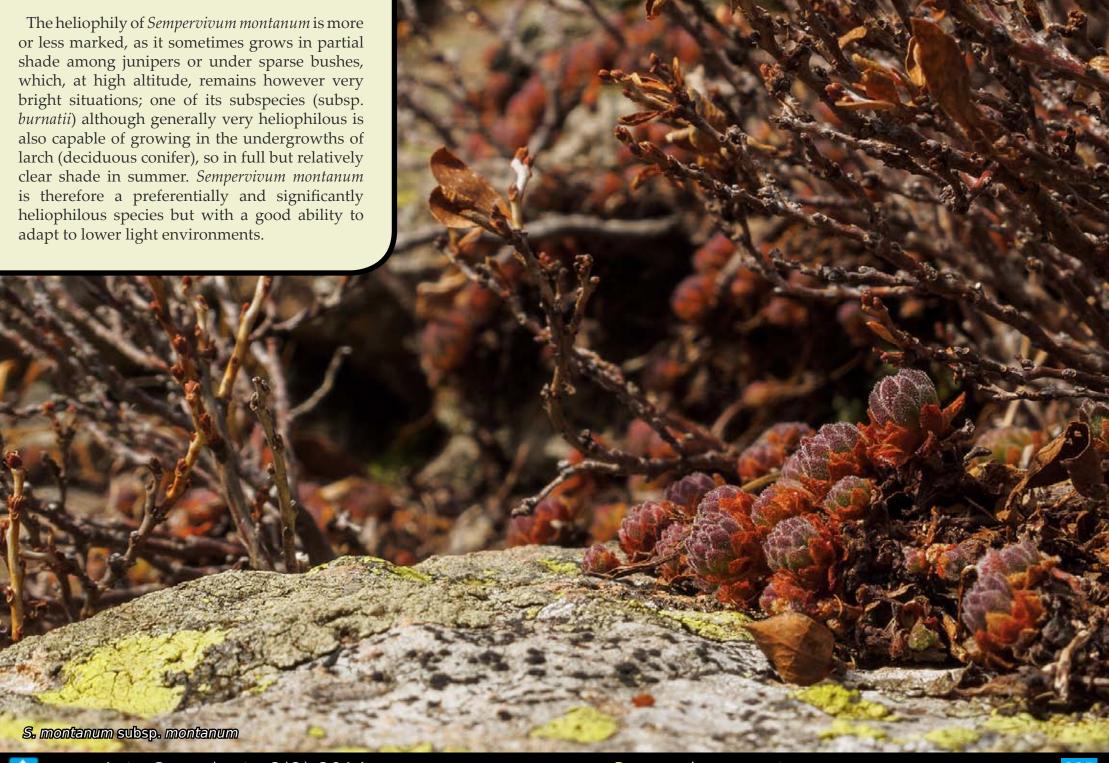
Regarding the vegetation levels, *Sempervivum montanum* is especially common in the subalpine and alpine belts and descends little in the mountain belt where it quickly becomes scarce. In the upper belts on silicate substrate, especially in the Alps, *S. montanum* often forms continuous and large populations and is extremely banal and is usually the predominant houseleek.



Sempervivum montanum occurs much more rarely at low levels than some of the other species with which it coexists frequently (*S. arachnoideum, S. grandiflorum, S. tectorum, S. wulfenii*). Only one of its subspecies (subsp. heterophyllum) was able to adapt to low altitudes in a limited area, with a very continental climate, where it grows on rocky islets in the forest as post-glacial relict.

Sempervivum montanum shows a strict acidophilia, one of the strictest in the genus Sempervivum. No natural location of *S. montanum* is known at this day elsewhere than on acid silicate rock (crystalline or volcanic). In the massifs mixing crystalline islets emerging from sedimentary layers (e.g. the Dolomites), *S. montanum* is only present on these islands and completely absent elsewhere.



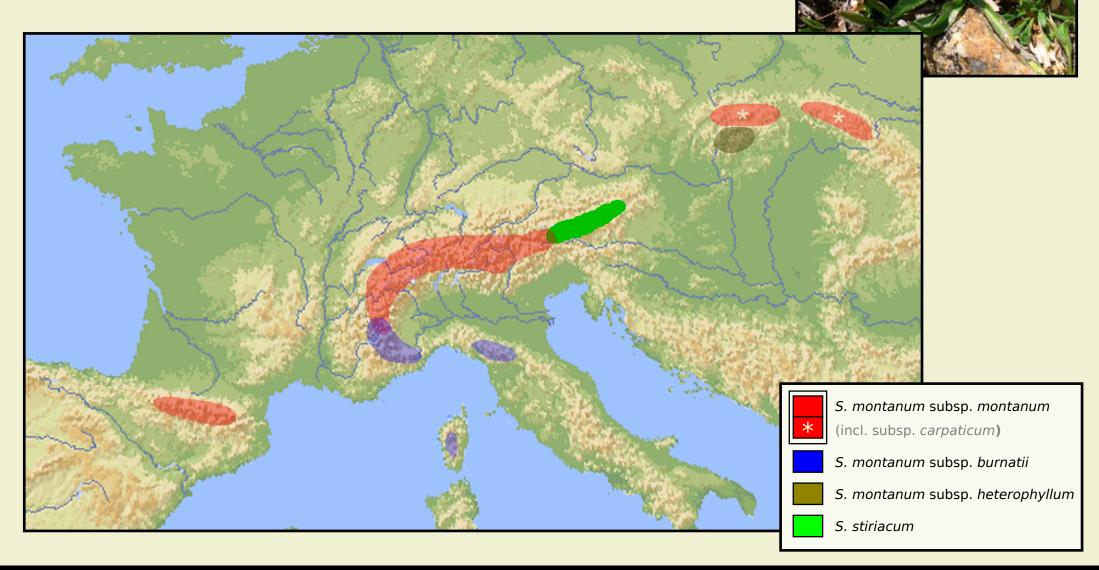




Distribution

Sempervivum montanum is a species with a very wide distribution since it is found from the west central Pyrenees up to the east of the northern Carpathians (in Romania), including the Alps and the northern Apennines, with a wide gap in the Eastern Alps where it is replaced by *S. stiriacum*.

Within this area, *Sempervivum montanum* is a very common plant and is present wherever the environmental conditions are consistent with its ecological requirements (sufficient altitude and silicate substrate).



Natural hybrids

As always with the houseleeks, studying Sempervivum montanum without taking into account its many natural hybrids would be neglecting an important part of the reality of this plant.

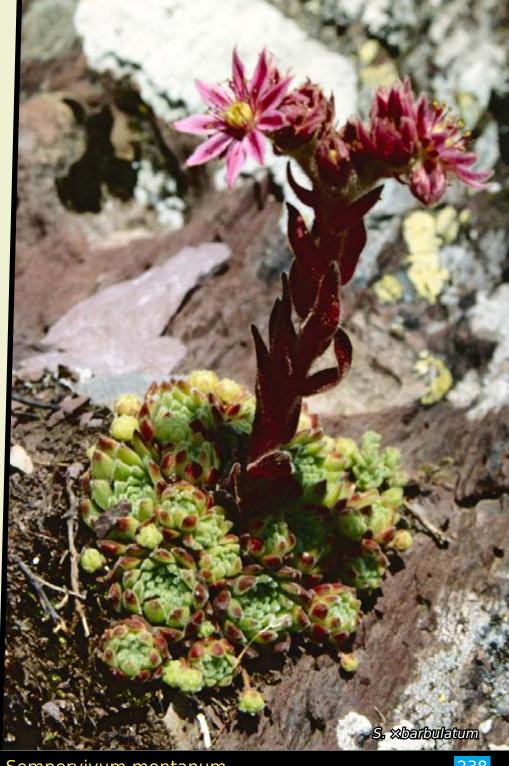
Sempervivum ×barbulatum Schott $(S. arachnoideum \times montanum)$

Sempervivum ×barbulatum Schott, Österreichische Semperviva, in Oesterreichisches Botanisches Wochenblatt Gemeinnütziges Organ, Vienne, 3: 91 (1853)

Synonymy:

- = Sempervivum ×ausserdorferi Huter
- = *Sempervivum* ×*delasoiei* C.B.Lehm. & Schnittsp.
 - *Sempervivum ×barbulatum* n-var. *delasoiei* (C.B.Lehm. & Schnittsp.) G.D.Rowley
- = *Sempervivum* × *fimbriatum* C.B.Lehm. & Schnittsp. (non Schott)
- = Sempervivum ×hausmannii Ausserdorfer ex Huter (non C.B.Lehm. & Schnittsp.)
- = Sempervivum × jeanbernatii E.G.Camus
- = Sempervivum ×lautareticum Lamotte
- = Sempervivum ×leucopogon Schnittsp. ex Lagger
- = Sempervivum ×macrantho-arachnoideum Jeanb. & Timb.-Lagr.
- = *Sempervivum* × *arachnoideo-macranthum* Jeanb. & Timb.-Lagr.
- = *Sempervivum* ×*montaniforme* Huter
- = Sempervivum ×pygmaeo-arachnoideum Jeanb. & Timb.-Lagr.
- = Sempervivum ×spurium E.G.Camus
- = Sempervivum ×timbalii E.G.Camus
 - ≡ Sempervivum frigidum [var.] timbalii (E.G.Camus) Rouy & E.G.Camus

Sempervivum ×barbulatum Schott is a nothospecific binomial name used to designate collectively the hybrids of type Sempervivum arachnoideum × montanum whatever the infraspecific taxa concerned of the parents, these latter can be quite varied because of the wide area of coexistence of these two variables species with a wide distribution. So we find this natural hybrid in the Pyrenees, the western and central Alps, Corsica and the Tosco-Emilian Apennine.



Sempervivum ×barbulatum is common where both parents live together. Note that it is the most common hybrid form of Sempervivum arachnoideum in the Pyrenees while in the western Alps it is rather Sempervivum ×piliferum (arachnoideum × tectorum) that is the predominant hybrid form; this phenomenon is probably due to a shift in flowering of Sempervivum montanum, its type burnatii, with slightly earlier flowering, predominating in the SW Alps.

Morphologically, *Sempervivum* ×*barbulatum* roughly holds the middle ground between both its parents and confusion with one of these is possible. According to the abundance or not of the hair of the hybrid individual concerned, confusion with *S. montanum* is sometimes possible, but it is mainly with a little hairy form of *Sempervivum arachnoideum* that it may occur, and, indeed the question often arises *in situ*, especially in the Pyrenees...





There is some confusion in some works between the spelling "barbulatum" (correct) and "barbatulum" (incorrect), this old confusion is maintained by the fact that each graphs has a coherent meaning (barbulatum = "with short and fluffy hair", barbatulum = "with scattered hairs").

Caution! In cultivation, you'll find most often under the name of "Sempervivum ×barbulatum" not a natural hybrid form of the type arachnoideum × montanum but a form of Sempervivum arachnoideum (a very nice form by the way) whose origin is not documented and is therefore a cultivar: Sempervivum 'Hookeri'.



Sempervivum ×christii Th.Wolf $(S. grandiflorum \times montanum)$

Sempervivum ×christii Th. Wolf, Notice sur quelques plantes nouvelles ou rares pour le Valais, in Bulletin des Travaux de la Société Murithienne (Société valaisanne des Sciences Naturelles), Sion, fasc. 16-18, «1887-89»: 29 (1890)

Sempervivum ×christii is a frequently occurring hybrid and is constant where the species cohabit or are in close contact. It's worth noting that S. grandiflorum presents its maximum frequency at lower altitudes than those where S. montanum flourish, so that S. ×christii often represents a link between the levels occupied by the two species, becoming the predominant or even the only species growing in some intermediate places and thus establishing a morphological and altitudinal pseudocontinuum between its two parent species.

Although intermediate between the two parent species, the aspect of this hybrid frequently reminds one more of Sempervivum grandiflorum (bigger and more open rosette, wider leaf) than of S. montanum. Outside the flowering period, confusion between S. ×christii and a small-sized S. grandiflorum is quite possible and common. The flower colour of this hybrid is rather variable, classically intermediate between the parent species, and thus yellowish-beige; specimens with pink flowers, or on the contrary, very pale flowers are frequent though. The distinction between S. ×christii and the possible white flowered forms of S. grandiflorum (likely back-crossings of this hybrid with S. grandiflorum) can be really complicated.

The natural area of this hybrid is the same as that of its parent *S*. grandiflorum: the concavity of the western part of the Alps, with a slight shift due to the tendency of this hybrid to climb higher than its parent.



Sempervivum ×rupicolum Kerner

(S. montanum × wulfenii)

Sempervivum ×rupicolum Kerner, in Oesterreichisches Botanisches Wochenblatt Gemeinnütziges Organ: 285 (1870); et 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. montanum and S. wulfenii (which is much more localized than it) because of the very similar requirements of the two species (high altitude, silicate substrate). *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's 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 is 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.

The natural area of this hybrid is the same is the same as that of its parent *S. wulfenii* in the Central Alps (it is absent from the eastern part of the area of *S. wulfenii* and from its low altitude locations due to the local absence of *S. montanum*).



Sempervivum ×schottii C.B.Lehm. & Schnittsp. $(S. montanum \times tectorum)$

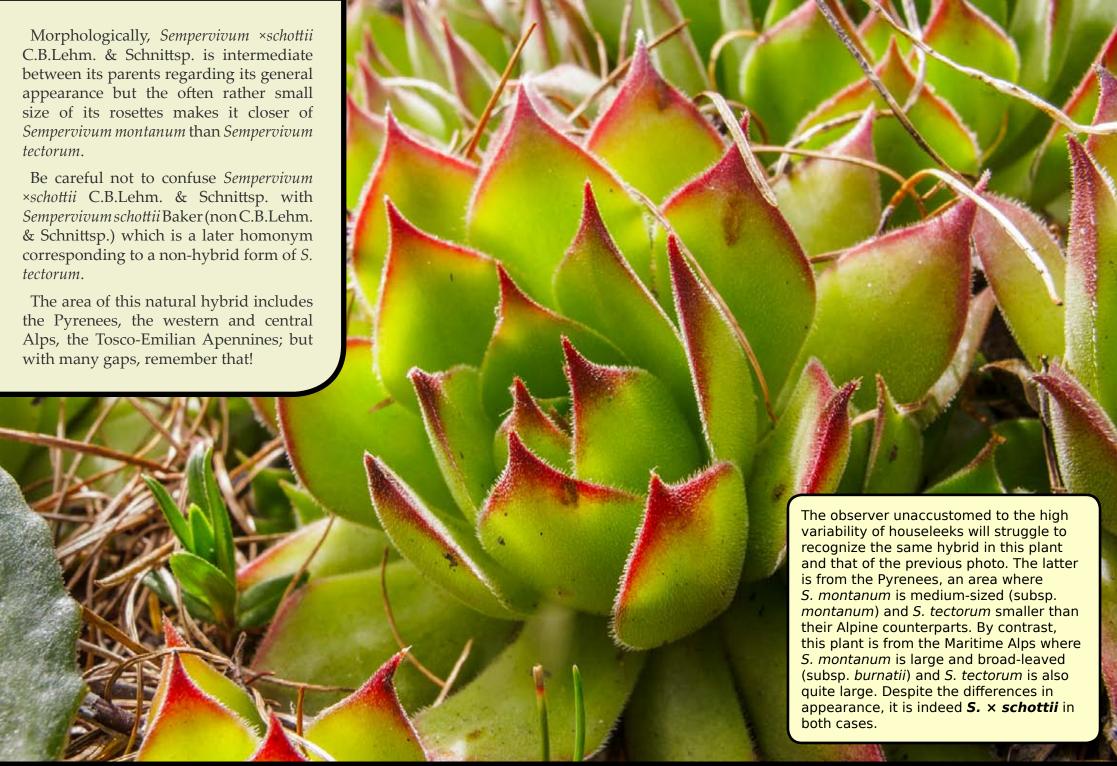
Sempervivum ×schottii C.B.Lehm. & Schnittsp., in Berichte Offenbacher Vereins Naturkunde 1: 35 (1860)

Synonymy:

- = Sempervivum ×adenotrichum Burnat
- = Sempervivum baeticulum Brügger ex P.J.Mitch.
- = Sempervivum baeticum Brügger ex Hayek
- = Sempervivum ×rhaeticum Brügger
 - *≡* Sempervivum ×schottii n-var. rhaeticum (Brügger) G.D.Rowley

Without being rare, Sempervivum ×schottii shows itself usually as isolated individuals here and there and not real populations as in the case of the aforementioned hybrids and especially Sempervivum ×barbulatum Schott (arachnoideum × montanum). The reason may simply be that among these three species (S. arachnoideum, S. montanum, S. tectorum) S. montanum tends to have in situ the earliest flowering (especially its subsp. burnatii) and S. tectorum has the later, what reduces the period of overlapping of parents flowering. In addition, the maximum frequency of the two parent plants is located at different altitudes, significantly lower for S. tectorum than for S. montanum, and their direct cohabitation is somewhat less frequent than in the case of the other species mentioned (but insects are in charge of transporting pollen from a distance).







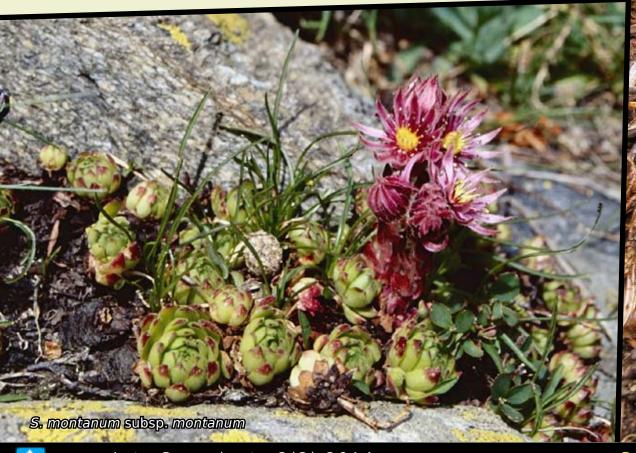


Cultivation notes

An attractive plant...

Sempervivum montanum, whatever the subspecies concerned and whatever the origin or the morphotype thereof, is a beautiful houseleek forming compact tufts of intense bright green often tinged with frost and purple at high exposures; the plant is particularly attractive when flowering because of its large flowers borne on short stalks.

Sempervivum montanum therefore appears to be a particularly interesting plant to keep in cultivation.



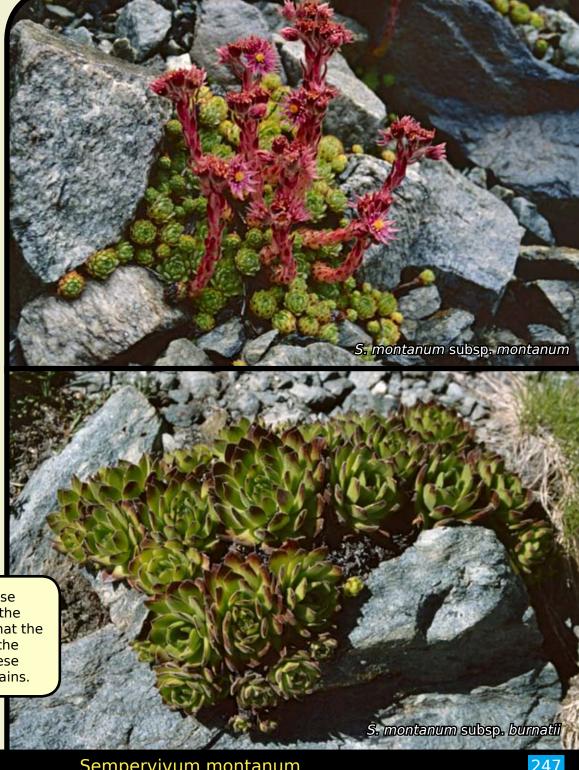


... but disappointing

Alas, Sempervivum montanum is one of the most disappointing houseleeks in cultivation in the plains. The problem is not a lack of vigour or a tendency to rot because, compared to some other houseleeks from high elevations, its vigour remains correct in cultivation at low elevation and it is relatively resistant to winter moisture (however it requires a protection under oceanic climate). No, the problem is that it is certainly the houseleek which deforms itself the most in cultivation at low elevation: it's difficult to recognize the same plant when you see it *in situ* and in cultivation: its stolons which are normally very short and hardly visible, lengthen like strawberry runners and colonize the neighbouring pots, even the rosette axes lengthen, not only the flower stems but also the axes of vegetative rosettes that become like a column with a tuft of green leaves above a long sleeve of old dry leaves...

In short, this plant in cultivation is often not very pretty and even downright ugly, let's face it; only its flowers are always beautiful which justifies keeping it in ornamental cultivation.

> It will be very difficult to maintain the aspect of these beautiful plants once introduced into cultivation in the plains, which is not surprising when you consider that the upper photo was taken in the Alps at 2,100 m and the bottom one at 2,800 m. Ecological conditions of these high altitudes are impossible to reproduce in the plains.



The reasons for the problem

What is the cause of this aesthetic disaster?

One immediately thinks of the lack of ultraviolet rays, very diminished in the plains because filtered by the thickness of the atmosphere compared to the natural locations of the plant at high elevation; this is probably one of the reasons but certainly not the only one and probably not the main one, because individuals of *Sempervivum montanum* growing *in situ* in undergrowth of larch (cf. supra) receive very little UV and present no such distortions.

In fact, the main cause of this kind of etiolating that is not really so (because it affects the stems but not the leaves) seems to be the insufficient

nycthemeral temperature range in the plains and especially the night temperatures that are much too high and allow nocturnal growth in length of axes that would normally be blocked *in situ* by the strong lowering down of night temperatures. This would require to be confirmed experimentally, but is probably the cause of the important deformation of *S. montanum* when it is cultivated in the plains.

This deformation is of course variable, depending on the area of cultivation and *S. montanum* will be much more beautiful and will show a much more natural appearance under a continental climate than under an oceanic climate.





Extreme temperatures

Although *Sempervivum montanum* is a houseleek coming from high elevation areas, high summer temperatures are relatively well tolerated compared to some other houseleeks: it does not like them but it will only yellow a bit and will stop its growth, but without much damage **until the night temperatures remain cool**.

Night temperatures above about 18-20°C for a prolonged time leads to metabolic suffering for the plants. In order to remedy this problem, it's better to reduce the exposition time to the sunlight of the rosettes, choosing the best situation for cool, night temperatures: the exposition E-NE.

It's important to water the plants regularly when the substrate is just dry, in order to avoid water stress during the hot periods. *S. montanum* tolerates prolonged water stress when the temperature is cool or cold by night, but it's a problem when the night temperature is warm. In these conditions, the water stress doesn't directly damage the plant, but it upset the thermal balance of the plant: the evaporation of the water through the stomata is the main way of thermal regulation of the plants, so for a houseleek which is suffering high temperatures it's better to avoid two things: 1) the prolonged closure of the stomata during the night, 2) the retraction of the rosettes, since the globular shape is the worst from the point of view of the heat exchange. We have only one solution: regular watering.

As for its resistance to frost, it is total: *in situ* this plant faces the rigors of winter in the Alps at almost 3000 m a.s.l. without any problem, so freezing at winter in the plains can only make it smile, but take care of the etiolation which of course decreases much of its resistance to low temperatures.

Propagation

As with all the houseleeks, sowing *Sempervivum montanum* is very easy and occurs spontaneously and massively in cultivation if you are not careful but the plantlets are often hybridised and therefore it's preferable to use vegetative propagation by planting daughter-rosettes, which are produced in abundance. In fact, given the tendency of the plant to lengthen its stolons in the plains, you'll spend your time planting rosettes in the original pots to try to keep the tufts as an aspect of... tuft.



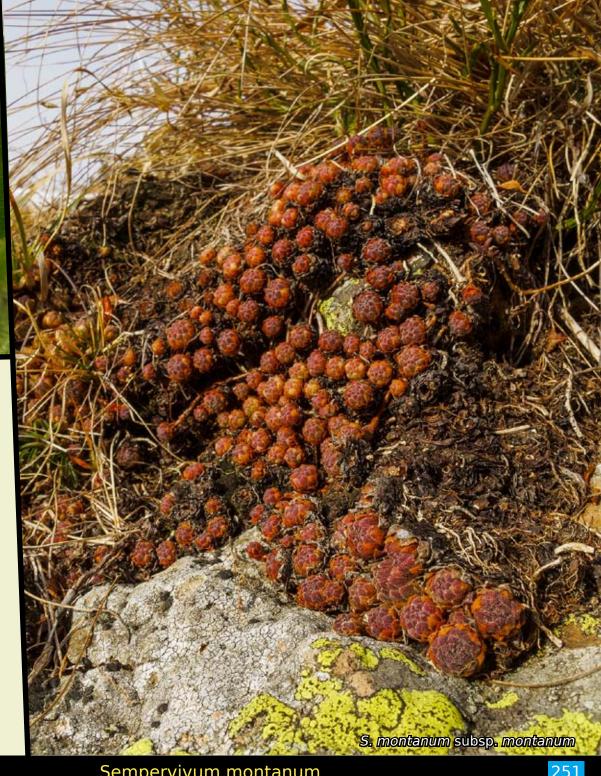
S. montanum subsp. montanum

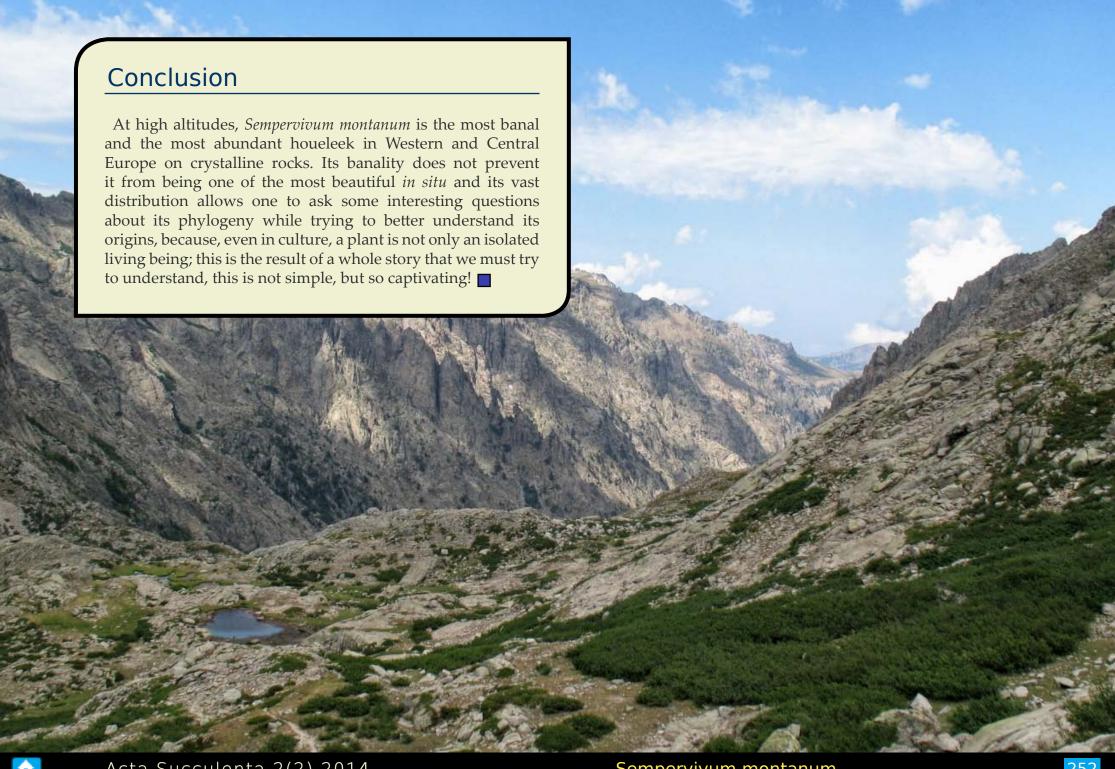


Where and how to get Sempervivum montanum?

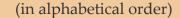
This species is in the trade plant list of nearly all the growers of hardy succulents and alpine plants. The subspecies heterophyllum is often a bit more difficult to obtain but it is present in the plant list of some specialized growers.

This plant being ubiquitous and very abundant in situ in high elevation areas, especially in the Alps, picking a few side rosettes in areas where the plant is not protected is not a problem for the plant and its environment.





To discover in the other online journals...





Avonia-News 7(6) [2014-06-06]

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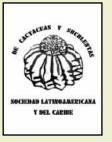
Pflanzenporträt: Orostachys malacophylla / Neue Taxa im Umfeld von Huernia saudi-arabica / Conophytum smaleorum.



THE CACTUS EXPLORER n° 11 [2013-04-05]

 $http://www.cactusexplorers.org.uk/Explorer11/Cactus\%20 Explorer11_complete.pdf$

The first *Lobivia / Borzicactus hoxeyi /* Nicaragua adventure */ Coloradoa mesae-verde / Maihueniopsis glomerata*.



BOLETÍN DE LA SLCCS 10(2) 2013 [2013-05]

http://www.ibiologia.unam.mx/slccs/www/pdf/Boletin/Vol_10_No_2_May-Ago-2013.pdf

Interacciones ecológicas / Apoyo a proyectos científicos / Expedición Long. 110 / Congreso Mexicano de Cact. y Suc. / Parque Nacional Desembarco del Granma / Comercialización de cactáceas nativas / *Thelocephala duripulpa* / Polen en *Rhipsalis lumbricoides* / Repuestas de Cereus aethiops / Germinação de *Hylocereus undatus* / Fungos fitopatogênicos de *O. ficus-indica*.



CRASSULACEA n° 3 [2013-04-15]

http://www.crassulaceae.ch/download.php?file_id=10275&download=true

Replacement type for Adromischus halesowensis.



ECHINOCEREUS online-journal 2(2) 2014 [2014-04-01]

http://www.echinocereus-online.de/Publikationen/Journal/EcJ-Online%202014%2002%20ov.pdf

Echinocereus fendleri subsp. fendleri / Echinocereus fendleri subsp. hempelii / Echinocereus fendleri subsp. kuenzleri stat.nov. / Echinocereus fendleri subsp. rectispinus.



JURNAL ACC AZTEKIUM n° 36 [2014-06-17]

https://files.acrobat.com/a/preview/29347d97-62f5-4600-b723-7850cfc38ac8

Pasiunea pentru Opuntioideae.



Sansevieria online 2(1) 2014 [2014-05-01]

http://www.sansevieria-online.de/lib/exe/fetch.php?media=hefte:so_2014_1.pdf

Die rätselhaften Früchte der Sansevierien / Madagaskar und seine Sansevierien / die Gattung *Sansevieria*, nom.cons. (Liliaceae) / *Sansevieria roxburghiana* von der Koromandelküste / *Sansevieria* - ein persönlicher Weg dazu..



SCHÜTZIANA the Gymnocalycium Online Journal 5(1) [2014-06-16]

http://www.schuetziana.org/downloads/Schuetziana_5_2014_1.pdf

A new subspecies of *Gymnocalycium kroenleinii* Kiesling, Rausch & Ferrari, and notes on the type form.



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Les Balsaminaceae / Chamaelobivia et Rebutia hybrides / Dracaena draco, une part de l'histoire des îles Canaries.



XEROPHILIA 3(2) / n° 9 [2014-06]

http://xerophilia.ro/wp-content/uploads/2014/07/Xerophilia-09-lq.pdf

Ariocarpus kotschoubeyanus / Sierra Corral los Bandidos / Ariocarpus agavoides and A. kotsch. var. albiflorus / Biosphere reserve / Turbinicarpus pseudomacrochele ×horripilus / A new Mammillaria / Turbinicarpus viereckii subsp. reconditus / Aztekium valdezii / Peru / African tour / Turbinicarpus mandragora / Little opuntioids / Crassula rubricaulis in NZ / variegated Carpobrotus edulis / Sedum fuscum.



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