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Diversity, Ecology, and Distribution of Opuntioideae (Prickly Pears and Chollas) Neophytes in Southern Switzerland

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Abstract: The invasion of Opuntioideae (cacti) was assessed at national, European, and global levels >14 years ago and requires an urgent update. At present, only three species of this subfamily are retained in the official list of the Swiss Federal Bureau of Environment, two of them being potentially invasive. About 550 new observations of *Opuntia* Mill. and *Cylindropuntia* (Engelm.) F. M. Knuth in the Swiss Cantons Valais, Vaud, and Ticino have been entered in the Swiss Info Flora database. Our observations include the revision of previously registered and new stations, using a revised taxonomy presented here. Our study covering the last 5 years reveals 12 species, each with a specific ecology. Four species have an invasive potential at a local level in the xeric Central Valais. We characterized the habitat of each species by bedrock and soil type, exposure, and microclimate. *Opuntia mesacantha* (ex *O. humifusa* Complex) and *O. phaeacantha* are currently invasive in the municipality of Sion. *Opuntia cymochila* (hitherto lumped with *O. phaeacantha*) is dominant in the municipality of Fully, and *Opuntia engelmannii* is expanding east of Fully. In Ticino and the Jura foothills, adaptations to 2–3-fold annual precipitation and limestone bedrock are explained by the different soil properties and root systems of Opuntias. Methods of control, in particular, the uprooting currently practiced in Fully and Sion, are discussed.

Keywords: *Opuntia*; *Cylindropuntia*; taxonomy; ecology; rock–soil–plant interactions; invasive species; climate change; control

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1. Introduction, Background

Opuntioideae species, represented in southern Switzerland by the genera *Opuntia* (prickly pears) and *Cylindropuntia* (chollas), are CAM (Crassulacaean Acid Metabolism) plants of the Cactaceae family with very efficient use of water that evolved in arid and semiarid areas of the Americas [1]. Here, we informally call them "Opuntias". The native habitat of taxa occurring in southern Switzerland extends from the semi-deserts of central and northern Mexico and the southwestern United States to the Great Plains of the Midwest and the wetter Atlantic coastal plains of southern Canada.

Opuntias are xerophytic and thermophile neophytes, originally introduced to southern Europe shortly after the discovery of the Americas. From southern Europe, several less cold-hardy species, such as *Opuntia ficus-indica*, *O. stricta*, and *O. dillenii*, were exported and have been cultivated in many subtropical and Mediterranean climates of South Africa, Australia, Asia, and South America, principally for fruit (prickly pears) and

cochineal dye production [2], living fencing [3], fodder [4], and medical use [5] (pp. 61–62). These less cold-hardy species are presently cultivated in gardens of the lake areas in Ticino (Figure 1); they may become potentially invasive with further climate change [6].

More cold-hardy species, such as *Opuntia humifusa*., *O. phaeacantha*, and *O. cymochila* were introduced from the Mediterranean area into southern Switzerland. The first occurrences in Valais were recorded between 1768 and 1788, first near the Lake Léman above Bouveret and Vouvry (Chablais, Figure 1) and then in the vicinity of the Château de Valère (Sion. Figure 1) [6–8]. Some of the species now present in Switzerland have been used for thousands of years as medicinal plants by the indigenous populations of North America [5] (pp. 61–62). Perhaps it was for this reason that monks brought them from the Mediterranean and cultivated them in the vicinity of religious sites. However, several species appear to have been introduced more recently [8].

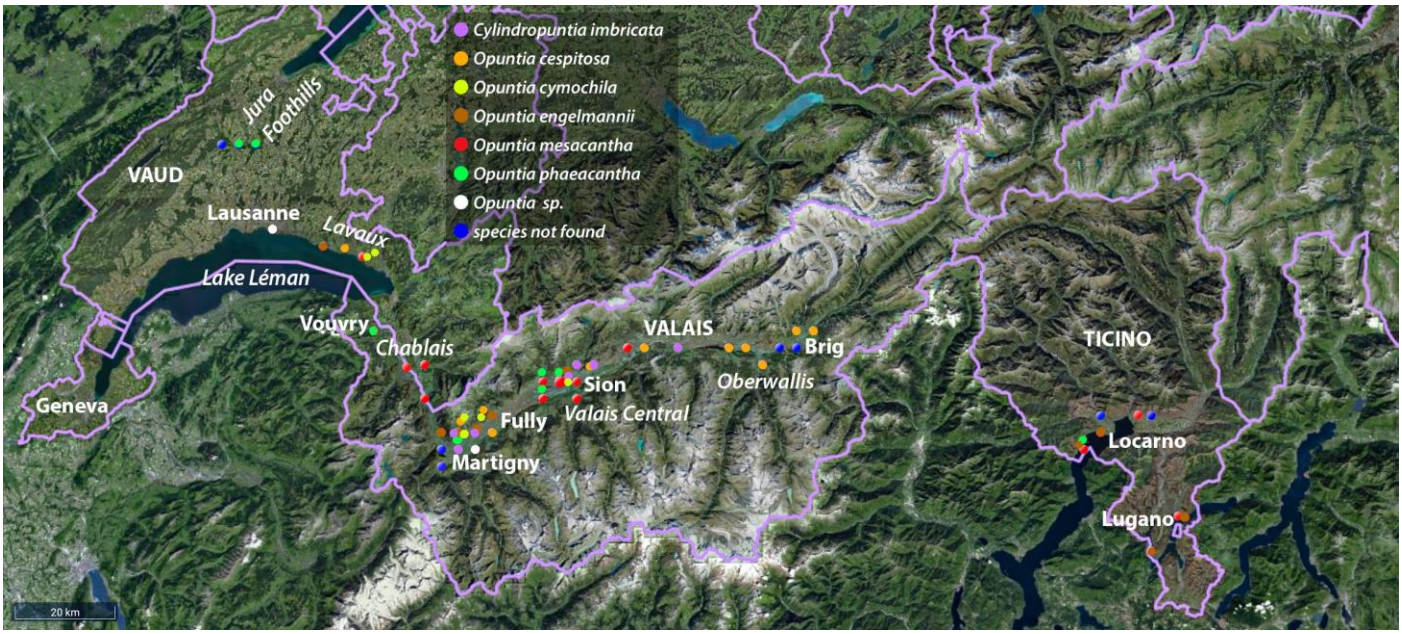

Figure 1. Approximate locations of the principal *Opuntia* and *Cylindropuntia* species in southern Switzerland and toponyms stated in the text. Cantonal/national boundaries in violet.

The invasive potential of Opuntias has been assessed at national [4,9], European [6], and global [10,11] scales. However, these studies all date from the first decade of the 21st century and urgently need to be updated. Most studies lack detailed morphologic comparisons with the native North American taxa. Hence, some of the distribution records have to be analyzed with caution [6] (p. 493). In particular, only two species (*Opunia humifusa* and *Cylindropuntia imbricata*) are mentioned for Switzerland in [6], based on [12]. So far, phylogenetic studies have focused on native Opuntioideae [13] (and references therein).

Opuntias were protected in Valais as a botanical curiosity between 1936 and 1998**.** Two species are now considered potentially invasive neophytes and appear in the list of problematic exotic species in Switzerland [14]: *Opuntia humifusa* and *Opuntia phaeacantha*. Removal campaigns were undertaken around 10 years ago in Valais on Valère Hill and in 2024 on the southern flank of the Mont d'Orge hill (Sion, Figure 2b). The municipality of Fully expressed concern about the presence of these cacti on its territory [15] and undertook uprooting in winter 2021–2022 in the Mont Rosel-les Follatères Nature Reserve and in 2023, notably of *O. engelmannii* at Les Planches de Mazembre (Fully, Figure 2a,d). According to our investigation, four *Opuntia* species are, at present, invasive in the municipalities of Fully and Sion, in the areas classified as "Dry meadows and pastures of national importance" [16] (Figure 1).

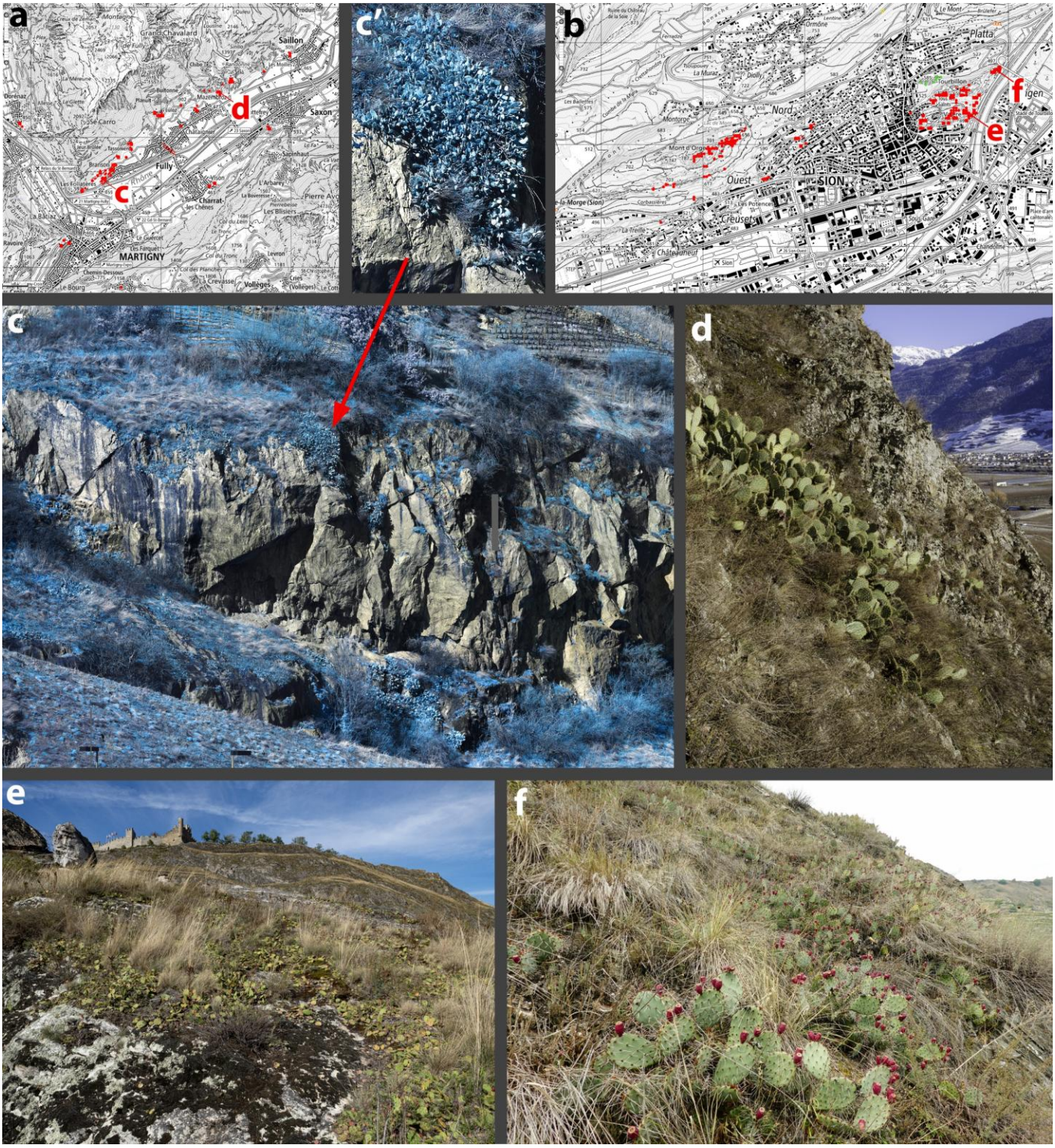

Figure 2. Localities with invasive Opuntias. (**a**) Map of the Fully community (Figure 1) with stations of Opuntias (red dots) and locations of figures (**c**,**d**) indicated. (**b**) Map of the Sion community (Fig-ure 1) with stations of Opuntias and locations of figures (**e**,**f**) indicated. (**c**) Photomosaic (original image size: 560 Mpx) taken with a camera detecting the infrared re-emission of chlorophyll, Grand Champ Rock, Branson, and *O. cymochila* in great abundance. (**c'**) Details of photomosaic, shown in high resolution, allowing for the determination of individual species (*O. cymochila*). (**d**) Invasive *O. engelmannii* east of Mazembroz. (**e**) Invasive population of *O. mesacantha* on the south slope of Valère Hill. (**f**) Invasive O. *phaeacantha* on a south-facing slope at the NE edge of Tourbillon Hill (Sion).

Currently, according to the list of Swiss vascular plants in ref. [17], only three species are present in Switzerland (*Opuntia humifusa*, *O. phaeacantha*, *Cylindropuntia imbricata*), while Desfayes [8] mentioned three additional species in his revision (*O. engelmannii*, *O. robusta*, *O. scheeri*). However, our recent study aimed at clarifying the invasive potential of these species [16] and showed that, on the basis of modern taxonomy, further species should be recognized in Valais. In such a context, the correct identification of species and varieties is fundamental, as each has a particular ecology and occupies a specific habitat. The correct recognition of phenotypic species and their ecology is an essential prerequisite for assessing their invasive potential. Recent observations have shown the rapid expansion of certain species since the work of Desfayes [8] and that, in the current context of global warming, expansion is likely to accelerate further still, with potentially colonizable surfaces on the increase.

The aim of this article is to refine the morpho-taxonomic revision of Opuntias, initially proposed for Valais occurrences [16], in preparation for planned phylogenetic work on Swiss Opuntioideae. We extend the report to other areas of Southern Switzerland (Cantons Vaud and Ticino, Figure 1). Here, we add new species discovered, particularly less cold-hardy species growing in Ticino. We analyze the ecology of Opuntias in the context of climate change, with warming values in the Central Alps being twice as important as the global average. We present and discuss new data on the substrate–plant relationships in areas with more humid climates than those found in Valais. Finally, we discuss control strategies, such as the uprooting of Opuntias presently practiced in Valais.

2. Materials and Methods

Some 1200 observations of the *Opuntia* and *Cylindropuntia* were listed for Switzerland by April 2024 in the Info Flora database: The vast majority of them (1080) are located in Valais, and only 45 are located in Vaud, 23 in Ticino, and 44 in other cantons (Figure 3b–d). These observations, particularly in Valais, often represent double or triple observations at the same stations by different observers over several years. All these observations are presently classified into four listed taxa:

1. *Cylindropuntia imbricata*, which is easy to determine with its upright growth and cylindrical cladodes.
2. *Opuntia humifusa*, which includes all creeping forms with few or no spines.
3. *O. phaeacantha*, which includes a variety of species with abundant spines.
4. *Opuntia* sp., retained by 390 observations (33%), partly covering other species not listed by Info Flora.

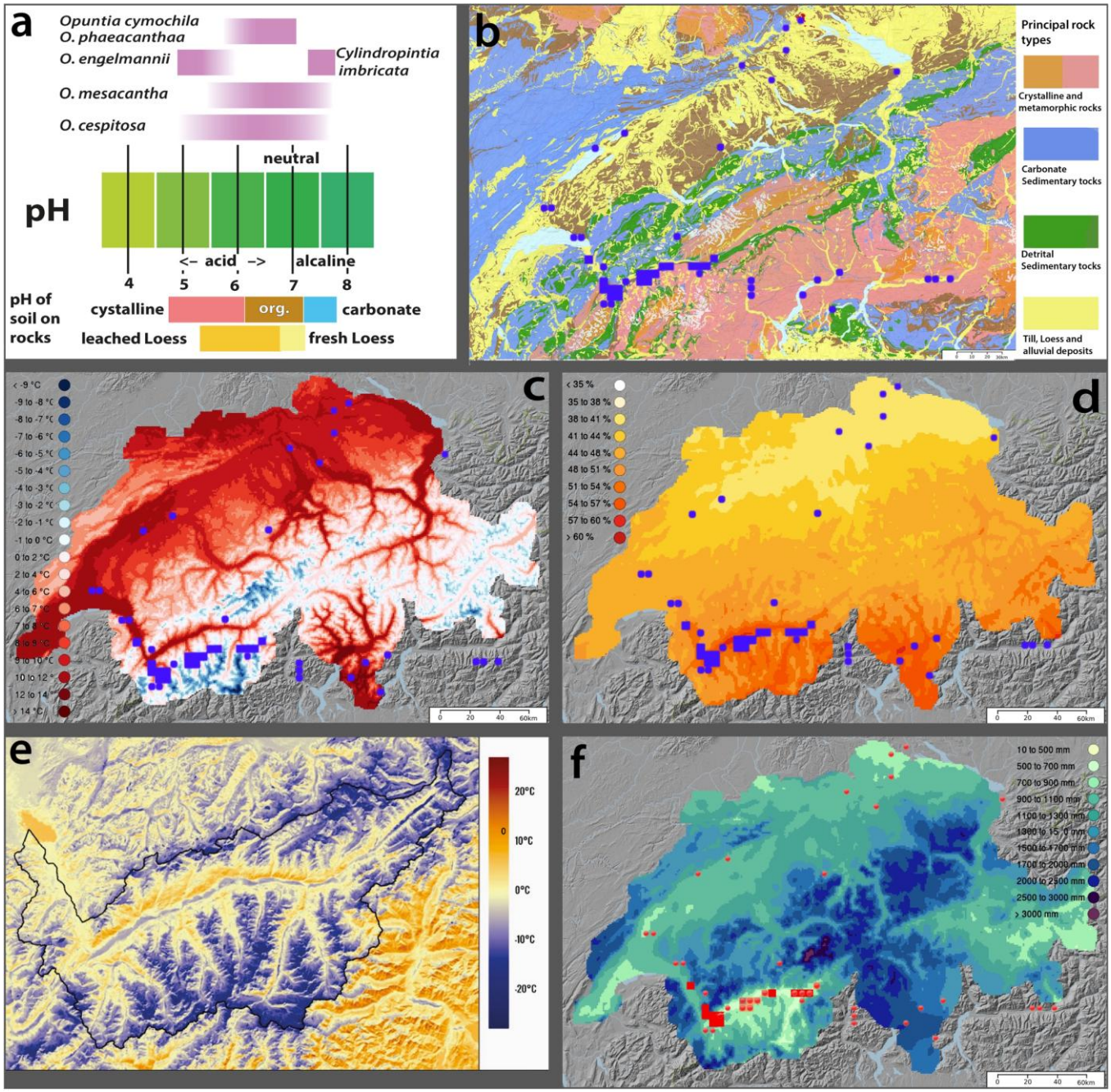

Figure 3. (**a**) Soil pH range (n = 24) measured in samples from the root space of the principal Opuntias (Figure A1). (**b**–**d**,**f**) Occurrences of "*O. phaeacantha*" and "*O. humifusa*" F in Switzerland according to IInfo Flora (Neophytes field book: https://neo.infoflora.ch/fr/index.html, accessed on 10 January 2025, superposed onto (**b**) principal rock types (Swisstopo:/https://map.geo.admin.c/#/map?lang=de&center=2587502.32,1207185.3&z=1.501&topic=geol&layers=ch.swisstopo.geologie-geotechnik-gk500-genese&bgLayer=void&featureInfo=default&catalogNodes=geol,1786,1787, accessed on 10 January 2025). (**c**) average temperatures, 1991–2020; (**d**) sunshine in %, 1991–2020. (**f**) annual precipitation, 1991–2020. Graphics from Swisstopo: (https://map.geo.admin.ch/#/map?lang=de&center=2660000,1190000&z=1&topic=meteoschweiz&layers=ch.bafu.gefahren-basiskarte,,0.7;ch.meteoschweiz.klimanormwerte-temperatur_aktuelle_periode, accessed on 10 January 2025). (**e**) Ground surface temperature on 6 January 2002, at 11:10. Only regions above 0 °C (yellow) are conducive to the survival and spread of Opuntias (eAtlas du Valais: landsat-7 ETM data; processing and mapping: V. Humphrey, IGD, UNIL).

During the work commissioned by the canton of Valais [8], all the known stations were visited, and a detailed survey was extended to the whole of Canton Valais, visiting sites with development potential for cacti. In 2023–2024, the survey was extended to Cantons Vaud and Ticino, presented here with preliminary data (Figure 1). It turned out that many of the plants observed belong to neither *O. humifusa* nor *O. phaeacantha*.

Accessions were collected and planted in a private garden in south-facing spots, sheltered from heavy rain above Lausanne (Figure 1) at 850 m elevation. The observation of these plants under conditions similar to those in the Valais enabled us to perform the following:

1. Observe the development of the different species under the same conditions.
2. Distinguish recent plantings of cladode cuttings from young plants grown from seeds or root remains.
3. Distinguish whether their propagation was by seed or propagules.
4. Compare specimens of the same species from different sites.

The correct morphological identification of the species was achieved thanks to close collaboration with the two co-authors, F L. Majure and D. J. Ferguson, who are specialists in North American Opuntias. Hundreds of images were exchanged, and herbaria were consulted to establish the taxonomy of the forms present in Switzerland. The taxonomic distinction is based on strictly morphological criteria, such as growth habit, shape, size, and color of cladodes; the arrangement of areoles and spines; flower color; and the period of fruit-bearing. Our species list does not represent systematic relationships between species, except for the *O. humifusa* complex.

Simultaneously with the plant collection, 26 soil samples were taken from the root volume of *Opuntia* plants to measure pH with the following procedure: 20 mL of dry soil was suspended in 40 mL of demineralized water by shaking for one minute. A stabilized pH was measured after 3–5 min with an accuracy of ±0.1 units. In the field, drops of 10% HCl were placed on soil samples to estimate its soluble carbonate content by observing the CO_2 development. Soil color and grain size were briefly described. In addition, the description of the ecology was completed with a determination of the bedrock, exposure to sunlight, and the type of vegetation associated with the individuals observed.

All observations were entered into the georeferenced Info Flora (National Center of data and information on the Swiss flora) database by means of the "carnet n ligne" (https://fieldbook.infoflora.ch/fr/observations, accessed on 10 January 2025) with one of the three listed species, or with *Opuntia* sp. for species not listed in the database. Our taxonomic identifications were recorded as new observations both in new stations and in previously known stations under the heading "Original name" in Info Flora. This taxonomic revision of most observations made prior to 2023 now totals some 541 new observations (Figure A1 on request from authors) for southern Switzerland, including just over a hundred new stations. All our observations, including the absences of plants observed previously, are documented by images uploaded with each observation to the Info Flora database.

Digital photography (macro-photos and high-resolution photomosaics with telephotos) was carried out with an Olympus (Shinjuku City, Tokyo, Japan) OM-D EM-5 III camera, , at 20.1 Mpx and 70 Mpx with pixel shift, and an Olympus zoom lens, 10–30., 1:2.8 pro, and an Olympus telephoto zoom lens, 100–400 mm pro, with a ×1.5 teleconverter. High-definition photomosaics (up to 2.6 Gpx) of sites with high *Opuntia* populations were assembled using Panorama Studio©. All photos ©Peter O. Baumgartner.

The toponymy of all localities is based on Swiss topographic maps (https://map.geo.admin.ch/, accessed on 10 January 2025). ID numbers in figure captions refer to the georeferenced observations registered in the Info Flora database (Appendix A on request from the authors). Dates are given in European format: dd.mm.yy. All scales are in cn.

3. Ecology of Opuntioideae in Southern Switzerland

3.1. Introduction

The Opuntioideae species of southern Switzerland dwell mostly on southern slopes of hills and mountains in clearings without important shade, or in vineyards. In Valais most occurrences are located on the south-facing right bank of the Rhône River (Figures 1 and 2). Most often, they occupy niches with a warm microclimate, on more or less steep slopes, under or above cliffs, or on stone walls between vineyards, facing due south or southwest. Despite multiple, recent introductions on a variety of substrates, their long-term survival and spread have been limited by the ecological requirements of the species concerned. The systematic monitoring of some 400 stations in the Info Flora database has shown that individuals planted on unsuitable substrates or in unsuitable microclimatic conditions have not survived. On the other hand, we need to keep a close eye on "hot spots" where a few species are proliferating, such as the hills of Sion, and the commune of Fully (Figures 1 and 2), which are discussed in detail below. With climate change leading to hotter, drier summers, the *Opuntia* species could proliferate rapidly. Hence, the importance of regular quantitative monitoring over the coming years:

3.2. Substrates: Rocks and Soils

Opuntias have extensive root systems in xeric habitats such as those of the Central Valais and Oebrwallis (Upper Valais) (Figure 1). Here, roots are often in direct contact with, or anchored in, crystalline bedrock. In contrast, in more mesic habitats, such as those of Ticino and the Lavaux and the Juta Foothills (Figure 1), the root system may be reduced, since constant humid conditions prevail in organic-rich topsoil. This adaptation has been confirmed by culturing Opuntias in places variably exposed to rainfall.

In general, bedrock determines the composition and granulometry of the mineral component of the soil. Mineralogical composition and organic matter (humus) content determine soil pH (Figures 3a and A1): An acid pH characterizes soils on crystalline rocks (Figure 3b, gneiss, granodiorite, and granite in Valais and Ticino). We measured a neutral to slightly alkaline pH in soils on carbonate-bearing detrital sedimentary rocks (Figure 3b, calcschist, sandstone, and conglomerate in the Sion hills (VS, Figure 2b)) and Lavaux (VD, Figure 1). These rocks are rich in quartz, phyllosilicates (clays, mica), and sometimes dolomite, a less soluble carbonate. *Opuntia* occurrences on limestone, as well as on dolomite and gypsum, show a slight alkaline soil pH and richness in calcium, which is tolerated by some of the currently represented *Opuntia* species but does not allow for their proliferation. However, there are *Opuntia* species that would probably favor calcareous substrates, and respond prolifically to them, but that are not currently present in southern Switzerland. Should they ever be introduced, such species could respond very differently from the species already present.

In large areas of the Rhône valley, the Jura Mountains, and in the low hills of Ticino, the bedrock is covered by glacial deposits (Figure 2b), either tillites composed of sand and gravel, or loess, a late Pleistocene proglacial eolian deposit. Yellow loess silts produce light brown, locally deep, nutrient-rich soils that are generally decalcified at the surface by rainfall, resulting in slightly acid pH values (Figures 3a and A1). These soils, highly prized for wine rowing, are also easily colonized by Opuntias. The presence of organic matter acts as a chemical buffer, resulting in more or less neutral pH values on various substrates (Figure 3a).

Populations of *O. cespitosa* and *C. imbricata* growing on dolomite–quartzite rocks are more tolerant to soils with a slightly alkaline pH (Figure 3a). Stations of other species, reported earlier on carbonate bedrock in [8] and by other observers for the Info Flora database have disappeared in Valais, showing that these species only lived there for a few years after their introduction, without being able to spread.

The soils rarely form a regular cover on the bedrock but are found in cracks or small rocky depressions, often produced by glacial erosion, from which the *Opuntia* root system benefits. Surprisingly, these soils retain a certain amount of moisture, thanks to (glacial) clays, [18] even in periods of drought. At the edges of vineyards, Opuntias benefit from a greater proportion of organic matter to proliferate.

In Ticino (near Lugano, Figure 1), we recently observed populations of a variant of *O. engelmannii* and *O. mesacantha* on rocky, siliceous limestone substrates. In the Jura Foothills and the Chanlais (Vaud, Figure 1), *O. mesacantha* and *O. phaeacantha* have normal vitality on limestone bedrock, whereas these species prefer acidic soils in Valais. This different adaptation must be related to the difference in the total amount and the seasonal occurrence of rainfall between Central Valais and the other areas (see Section 3.6).

3.3. Climate and Climate Change in Alpine Switzerland

- Temperatures

Global warming (2023) in Switzerland, at +2.4 °C since pre-industrial times, is more than twice as high as the world average of +1.1 °C for the same period. According to the MeteoSuisse [19] measuring stations, the rise in air temperatures has accelerated in Switzerland since the 1980s. Hence, the modern climate is favorable for the survival and spread of certain *Opuntia* species throughout the Alpine valleys, the low elevations of the Swiss Plateau, and the foothills of the Jura Mountains (Figures 1 and 3)

Central Valais, placed within the Central Alps, shows a temperature increase greater than, for example, in Lucerne, north of the Alps (Figure 3c), and mean summer temperatures in Sion gradually approach those of Ticino (Lugano) ([16], Figure 21a). In Sion, mean annual values rose above 10 °C as early as 1990. Monthly values for 2003–2022 at the Sion station show that the June–July–August maxima first reached in 2003 were again reached in July 2006, July 2015, and July 2022 [19].

Overall, summer temperatures have been on average above the standard 1991–2020 period since 2010. The precocity of spring development in Switzerland changed radically around 1990 [20]. Since then, spring development has been occurring earlier and earlier. These changes favor the early blooming and fruit ripening of Opuntias, and thus their fertility.

For thermophile species, minimum temperatures seem to be the limiting factor for their naturalization. However, with a few exceptions (e.g., St-Léonard, VS), Opuntias are not affected by the cold air sinks that form at the bottom of Alpine valleys during calm winter nights. In dry conditions, most species can tolerate winter temperatures of −10 to −15 °C without harm. But southern exposure, with generous winter sunshine, probably helps them to survive through such cold periods (see below).

- Sunshine

Direct sunlight is a fundamental condition for the survival of all the species investigated. Our in-habitat measurements show that sunlight enables the cladodes to warm up to 12 °C above ambient temperature, guaranteeing metabolic activity even on cool, sunny days in spring and autumn. Cold winter weather induces the production of anthocyanins in the sun-exposed epidermis of *O. mesacantha* cladodes, resulting in a red color and thus favoring the absorption of infrared radiation. The same species, and to a lesser extent *O. cespitosa* and *O. cymochila*, exhibit the winter wrinkling of cladodes resulting from the reduction in tissue water, thus preventing freezing.

Cultivation in a greenhouse or in shade results in lower growth rates, the elongation of cladodes, and less or no flowering. In some species (*O. mesacantha*), the shape of the cladodes is a good indicator of sunlight quality, i.e., with enough UV, cladodes growing in the shade, in the garden, or in the greenhouse increase their exposed surface area by developing an elongated shape ([16], Figure 19f).

Valais and Grisons are the sunniest regions in Switzerland (Figure 3d), but *O. mesacantha*, the most tolerant species, has been observed also in northern Switzerland with much lower average sunshine (Figure 3d). Winter sunshine appears to be particularly critical for the long-term survival of Opuntias, as it heats up the soil on south-facing slopes, rapidly melting any snow. This phenomenon is illustrated by a satellite snapshot of ground surface temperatures on 6 January 2002, at 11:10 a.m. (Figure 3e): only regions above 0 °C are prone to *Opuntia* proliferation. Since then, sunshine duration has risen sharply, especially in Central Valais (Figure 3d).

- Precipitations

The Central and Upper Valais are the dryest areas of Switzerland with average values of annual precipitation below 600 mm/year (Figure 3f), favoring the spread of diverse *Opuntia* populations. In contrast, the Chablais, ths Swiss Plateau, and the Jura foothills (Figure 1) hosting scattered *Opuntia* occurrences yield average values between 900 and 1300 mm/year. The area of Ticino is extreme with *Opuntia* occurrences in areas with average values between 1500 and 2000 mm/year (Figure 3f, [19]). On the other hand, the annual precipitation recorded between 1865 and 2020 has not changed significantly in Switzerland ([16], Figure 21b). The increasing aridity observed over the past three decades in Valais results from rising temperatures and longer periods of drought, resulting in increased evapotranspiration, and occasional strong rainfalls rapidly drained by occasional catastrophic runoff.

3.4. Opuntia Vitality and Interaction with Local Vegetation

The period of strong growth, flowering, and fruiting lasts from April–May to June–July. This is followed by a period of dormancy in hot, dry weather, which can be interrupted by summer rains. In spring, herbaceous plants compete with Opuntias for light. As a result, early mowing greatly favors them.

The vitality of each species depends largely on its adaptation to the substrate (soil pH, presence/absence of carbonates), sunshine, microclimate, and soil water reserve (in xeric situations). It is the species' natural habitat in North America that determines its habitat in Valais. *O. cespitosa* adapts to the more mesic conditions, followed by *O. mesacantha* and *O. cymochila*, while the larger species, *O. phaeacantha*, *O. engelmannii*, *O. scheeri*, and especially *C. imbricata*, do best in xeric sites. In contrast, *O. phaeacantha* and *O. engelmannii* have adapted to the 2–3 times higher annual precipitation in the Jura foothills and Ticino (Figures 1 and 3f).

Small, creeping Opuntias (*O. mesacantha*, *O. cespitosa*, *O. cymochila*) or cushion Opuntias (*O. fragilis*, *O. polyacantha*) share the same habitat as other xero-thermophile species, such as *Sempervivum* spp. and *Sedum* spp. with which they may compete. These same species can also compete with dry grassland flora, particularly if the latter is stressed by prolonged and more intense droughts, which have become increasingly frequent in recent decades. In general, well-developed dry grassland is unlikely to be replaced by Opuntias, as it provides shade for the creeping species, limiting their development. However, on the southern slopes of Valère Hill (Figure 2b), *O. mesacantha* massively colonizes the edges of soil-filled rocky depressions covered with grassland (Figure 2e). Old cladodes and tuberous roots ([16], Figure 19b) of this species can be densely present in the soil under grassy patches, where they compete with the roots of herbaceous species while developing aerial cladodes above plant-free soil or rocks (Figure 2e). The strong presence of Opuntias can potentially cause the early drying out of low-volume soil pockets, jeopardizing the fruiting and survival of herbaceous plants in late spring.

On the other hand, rising species such as *O. phaeacantha* are not influenced by the shade of tall grasses; they proliferate (Figure 2f) and compete with the latter at root level. Finally, species forming ascending bushes (*O. engelmannii*, *O. scheeri*) colonize steep grassy slopes or rocky cracks and flats facing south or southwest (Figure 2d). They cohabit with

herbaceous plants, most often *Arthemisia* spp. They do not compete directly for light with the latter, as they cover only a small area of the ground.

3.5. Propagation Strategies

Most species multiply by both asexual propagules and seeds. Young *O. fragilis* cladodes detach from the parent plant at the slightest touch. This is also the case for *O. mesacantha*. For these species, dispersal occurs by gravity on steep slopes, or by barbed spines that attach easily to the fur of small mammals dispersing the cladodes. For the other species, we observed many young plants with the morphology of seedlings, with an initial cylindrical stem resulting from seed germination, quite distinct from that of recently planted cut cladodes.

Almost all species flower in Valais, and the flowers are pollinated by a multitude of insects: bees, bumblebees, and beetles. Self-fertilization (agamospermia) and self-compatibility during pollination are frequent [21]. Fruit ripening takes place in autumn or early winter, and then fruits fall off spontaneously or remain on the cladodes until the next flowering period (e.g., O. *humifusa* Complex). The ellipsoidal fruits roll easily and disperse by gravity downslope from the mother plant. In the clear case of *O. engelmannii*, the juicy ripe fruits are ingested by birds, and the seeds are dispersed with their droppings, e.g., in the cliffs above Mazembroz (Figure 2a,d). The Common Raven (*Corvus corax*) was reported as an important *Opuntia* fruit consumer and thus seed disperser on Teneriffe [22] and Menorca [23]. This species nests in the cliffs above Mazembroz. When entering the fruiting population of *Opuntia engelmanni* above Mazembroz in November 2021 (Figure 2d), the local couple of Ravens had a "controlling attitude".

According to [23], the viability of germination of *Opuntia* seeds does not statistically increase by their passage through the digestive tract of vertebrates. However, according to the study, endozoochoran dispersal is important for uphill colonization along steep rocky slopes.

Dispersal over long distances by birds was revealed in a study [23]. Particularly important is the observation of the European Starling (*Sturnus vulgaris*) ingesting fruit of *Opuntia maxima* at Cap Creus (Catalonia). This bird is very common and migrates between central and southern Europe (its winter habitat). Opuntia seeds could well be introduced from the Mediterranean realm into southern Switzerland during spring migration and geminate if the bird's droppings fell in the right environmental conditions.

3.6. Opuntia Adaptation to Mesic Conditions—Discussion and Conclusions

Compared to Central Valais, the Chablais and the Jura foothills receive twice as much annual precipitation. For Ticino, annual rainfall is up to three times more. It is in the latter areas, where acidophile species, such as variants of *O. engelmannii* and *O. phaeacantha* occur on limestone bedrock. Our interpretation of this relationship is that the influence of bedrock on topsoil pH is a function of the ratio between precipitation and evapotranspiration. On limestone in Valais, during hot summer periods, the evaporation from the topsoil causes capillary rise in water rich in dissolved carbonates from the bedrock. This process maintains a high pH even in organic-rich soils and keeps the soil saturated with calcium at the surface, creating unfavorable conditions for most Opuntias. In contrast, in the Jura foothills and Ticino regular precipitation, particularly in summer, leaches particulate carbonate and dissolved calcium out of the topsoil, lowering its pH [24]. As mentioned above, the *Opuntia* root systems are much less developed in these more humid areas and generally do not reach down to the bedrock. In addition, soil profiles on karstified limestones are generally well drained. They lack silicate sand or gravel but may be enriched in residual clays derived from limestone dissolution, creating a barrier for the rise of calcium-rich waters.

In conclusion, by adapting their root system to mesic conditions, Opuntias probably do not achieve contact with calcium-rich pore waters, allowing their normal vitality.

On the other hand, the presence of dissolved silica (silicic acid, $Si(OH)_4$) in soils derived from the weathering of clays and other silicates appears to be essential for the proliferation of Opuntias, as they contain significant quantities of opal phytoliths. In addition, Opuntia essential oils contain cyclic oligosiloxanes [25].

4. Invasive Species Management and Control

A recent report [25] discusses global actions for the management of cactus invasions. The report points out the importance of early detection and species identification upon introduction and the evaluation of its invasive potential in a given environment. Global climate change is causing excess warming in the Alpine region [19], calling for proactive actions from the local entities responsible for invasive species. The decrease in frost probability opens the way into the South Alpine ream for less cold-hardy species that are invasive in the Mediterranean (e.g., Opuntia *ficus-indica* in Ticino).

At present, of the creeping species, *O. mesacantha* is invasive in Fully and Sion (Figure 2b,e) and some spots in Ticino. Regarding spreading species with some upright growth, *O. phaeacantha* is abundant in the municipality of Sion (Figure 2b,f), while *O. cymochila* is dominant in the municipality of Fully (Figure 2a,c). Of the upright species, variants of *O. engelmannii* are very present and expanding east of Fully (Mazembroz, Figure 2b,d) and in a few places along Lake Lugano, TI. Currently, the other species have no invasive tendency but should be monitored.

The current distribution of the most common species (*O. mesacantha*, *O. cespitosa*, *O. cymochila*, *O. phaeacantha*, and variants of *O. engelmannii*, Figure 1) shows that in Valais, each species has a rather separate realm. Despite their initially random introduction, this distribution seems to be the result of survival and dispersal depending on the optimal substrate and microclimate for each species.

4.1. Current Management Unintentionally Encourages Proliferation

Faced with the threat of the *Opuntia* invasion of steppe grassland and rocky outcrops, and the fear of the regression, or even disappearance, of certain native species, the municipalities of Sion and Fully have begun to intervene by uprooting Opuntias. However, our observations show that this approach may be counterproductive. In fact, it produces bare ground that favors massive seed germination and the recovery of small root or cladode remnants.

1. South slope of Valère Hill (Figure 2b), visited on 2 February 2022. An area in which the soil had been stripped bare following a cleaning operation some 10 years ago shows an abundance of *O. mesacantha* similar to neighboring areas, in which no intervention was carried out. In the treated area, the herbaceous appearance is more vigorous and the composition is different from the treated areas, where we found numerous *Opuntia* seedlings.
2. At Les Follatères (Figure 2a), in an area of 200–300 m^2, several *Opuntia* species found in Valais were planted "in a botanical garden", and most were thriving. The Opuntias were removed from this area during winter 2021/2022, leaving bare ground. On 30 June 2022 and 16 July 2024, a large *O. engelmannii* shrub had been spared. The examination of the treated area in 2024 revealed several fruiting *O. cymochila* and *O. engelmannii* plants, probably re-grown from root remains in just 2 years.

Similar observations of recovery after the removal of *O. engelmannii* were made in summer 2023 at Les Planches de Mazembre (Fully Figure 2b) and in summer 2024 of *O. mesacantha* at Mont d'Orge (Figure 2b). Future monitoring should show the resilience of the various species.

Clearly, a single uprooting operation cannot eliminate Opuntias. It damages indigenous species sharing the same root space and denudes the soil, encouraging seed

germination and the recovery of even the smallest remnants of *Opuntia* roots, particularly of small creeping species.

Other maintenance activities are likely to encourage the spread of these species. One example is the mowing of roadsides and footpaths, which is current practice in many municipalities. Observations, particularly in Fully, show that south-facing roadsides are an ideal habitat for *O. mesacantha* and *O. cymochila*. Mowing in spring or early summer removes the shade produced by tall grasses and encourages the growth and blooming of Opuntias. Mulching conserves moisture and enriches the soil. This process favors both herbaceous plants and Opuntias. If mowing is carried out close to the ground with string trimmers, the Opuntias are cut into pieces, and each piece of cladode can root and form a new plant. This phenomenon can typically be observed in the municipality of Fully.

4.2. Deliberate Planting

Recent (2019–2022) planting of cut cladodes has been observed in several locations, particularly with large species, notably *O. engelmannii*. These plantings are easily recognized by a large, partly buried cladode often surrounded by an arrangement of stones. Such observations have been made on the southern slopes of Valère Hill, and in the municipalities of Dorénaz and Fully (Figure 2a). Many plantations are also located on private land (abandoned vineyards, wasteland, gardens), which is often inaccessible. It is therefore necessary to raise public awareness by explaining the risks these plantations represent for the native vegetation [26]. Nevertheless, some recent, isolated introductions could be the result of dispersal by birds, migrating northward form the Mediterranean in spring (see Section 3.5).

4.3. Managing and Controlling Opuntia Populations

Since simple uprooting proves ineffective, other actions need to be considered. But before tackling all populations, it is necessary to assess the invasive potential of each species in the different habitats on a case-by-case basis.

- Rare and scattered presence of species

In many cases, plants are now present in small, scattered populations. This is the case for *C. imbricata*, which occupies specific niches of very limited extent, currently with minimal potential for propagation. However, this genus and the related genus *Austrocylindropuntia* Backeb. are invasive in Portugal, Spain, and southern France [26]. Concerning the Oberwallis (upper Valais) stations, *O. cespitosa*, the only species widely distributed in this area (Figure 1), some dispersal has been observed around the surveyed stations, but it remains localized. A visit in 2022 to historic stations listed in the Info Flora database (under the name *O. humifusa*) observed no clear progression. Watch is recommended, but no action seems necessary at present.

The few stations in the Chablais, from Martigny to Vouvry, are rather anecdotic. The station in the municipality of Vésonnaz, above St-Maurice, on siliceous sediments, reveals individuals of *O. mesacantha* of low vitality, on the verge of extinction. A station of *O. phaeacantha*, cultivated in Vouvry between concrete walls, is performing very well, whereas a cutting found 60 m further on in a rockery, probably on lime-rich soil, has very poor vitality. This example shows that propagation can be seriously limited by the substrate. However, these sites should be monitored annually, as the spread of the species may increase with climate change, and recent plantings of *O. engelmannii* above Dorénaz, on siliceous rock, should be eliminated. The region between Vouvry (Figure 1) and Le Bouveret was examined because, according to historical sources [8], *O. mesacantha* was introduced there. Not only are the cliffs calcareous, but they are not well exposed. In addition, the slopes are now heavily wooded, ruling out the presence of Opuntias; no individuals have been found in this area.

Scattered occurrences of *Opuntia mesacantha*, *O. cymochila*, *O. phaeacantha*, and a variant *of O. engelmannii* have been observed on rocky ledges and cliffs in Lavaux and the Jura Foothills. They have adapted to 600 to 1100 mm of average annual rainfall and 12–25% less average sunshine (Figure 3). The species have a normal vitality, but propagation is limited by labored vineyards in the Lavaux and by forest growth in the Jura Foothills.

Based on preliminary observations in Ticino, the occurrence of Opuntias seems very spotty. They have to cope with 1300 to 2000 mm average annual rainfall (Figure 3), which is 3–5 times the Mediterranean average [23]. Nevertheless, *Opuntuia m*esacantha of the *O. humifusa* Complex is locally invasive on gneiss rocks polished by Quaternary glaciers, first colonized by mosses that provide a thin humus substrate for *O. mesacantha.* A variant of the *O. engelmannii* aggregate, probably related to O. *engelmannii* var. *cuja* (see taxonomy, Section 6)) seems to be well adapted to cliffs and stone walls of siliceous limestone. This taxon must be monitored; it could rapidly expand by bird dispersal along Lake Lugano and Lago Maggiore, where this less cold-hardy plant is now rarely threatened by frost.

- "Hot spots" of massive proliferation

Action is needed to control the "hot spots" of massive proliferation. As detailed above, these sites are in the Fully (Branson, Saxé, Mazembroz. Figure 2a) and Sion (Mont d'Orge, Valère, Tourbillon, Figure 2b) municipalities (Figure 2). Observations in recent years, well documented in the Info Flora database, show a significant increase in populations, further accentuated during the hot, dry summers of 2022–2023.

On the rocks of the south-facing slope of Valère (Sion), the steppe grassland is losing ground because of early drying, which is encouraging the proliferation of *O. mesacantha* (Figure 2b,e). In fact, according to our observations, global warming and the ensuing drought seem to favor Opuntias, to the detriment of native grasses and other species. At the eastern end of Tourbillon hill, *O. phaeacantha* cover can reach 30% (Figure 2f). Mowing should be abandoned, as tall grass, even when dry, provides shade, limiting the vitality of creeping species.

Opuntia phaeacantha and *O. mesacantha* proliferate on the partly inaccessible cliffs of Tourbillon's southern flank (Figure 2b). Opuntias cling to flats and fractures in the cliffs, where they compete with *Sedum* and *Sempervivum* species, currently not threatened in Switzerland. Controlling them in these areas seems to me to be very difficult and, at any rate, very costly, but probably not essential for maintaining local biodiversity.

On the Mont d'Orge hill, *O. mesacantha* and *O. phaeacantha* proliferate on steep, south-facing grassy slopes that are often difficult to access. Recent uprooting (spring 2024) has eliminated most of the plants, but some root remnants have regrown.

Opuntia cymochila and *O. mesacantha* have taken over abandoned vineyards, roadsides, rocks, and vineyard walls in the Fully municipality. To limit the vitality of these Opuntias, we strongly recommend mowing grass late or not at all.

The Grand Champ Rock (Branson, opposite the Rhone bridge) is covered with a very dense population of *O. cymochila* (Figure 2c). There are also a few shrubs of the red variety of *O. phaeacantha* and *O. mesacantha*. This station has a tourist appeal highlighted by images on numerous websites addressed to hikers. Removal campaigns have achieved limited success in the Follatères reserve and around Branson. The cladodes should be cut at ground level to preserve the herbaceous plants.

Variants of *O. engelmannii* have proliferated in the cliffs above Saxé and Mazembroz (Figure 2d). These areas are difficult to access. On the other hand, this upright species takes little ground space and does not threaten herbaceous plants. The uprooting campaign carried out by the Fully municipality in spring 2023 eliminated the most accessible plants, but we observed a recovery of root remains.

In conclusion, for the municipalities of Sion and Fully, we recommend identifying the areas in which control action is needed. This should be followed-up with and repeated

over several years, with interventions that spare other species as much as possible. Other areas at risk of proliferation will need to be monitored over the coming years.

5. Conclusions

The examination of the about 400 stations of the *Opuntia* and *Cylindropuntia* genera known prior to this study (Info Flora database), as well as the identification of numerous new stations, enabled us to clarify the taxonomy, ecology, biogeography, and local invasive potential of species of these genera in Valais, Ticino, and Vaud. For the first time, the morphotaxa of Swiss Opuntioideae are based on detailed comparisons with native taxa, thinks to collaboration with North American specialists. This prepares the stage for phytogenetic comparisons between native and introduced taxa in Europe:

- The five *Opuntia* species most present in Valais and Ticino clearly show naturalization conditioning by climate and substrate, despite an initially random introduction: *O. mesacantha* of the *O. humifusa* Complex is invasive in Bas-Valais and in Central Valais as far as Sierre. *O. cespitosa* is restricted, with a few exceptions, to Oberwallis, perhaps due to its preference for more mesic conditions. Invasive occurrences of *O. cymochila* and variants of *O. engelmannii*, thermophilic species, are practically restricted to the municipality of Fully. Invasive *O. phaeacantha*, a xerothermophilic species, is practically restricted to Mont d'Orge and the hills around Sion.
- *O. phaeacantha*, *O. mesacantha*, and variants of *O. engelmanni* have adapted to humid climates in Ticino and the Jura foothills by reducing their root system to the humus-rich topsoil, which leaches from carbonates and is regularly humidified.
- *O. mesacantha* is the most adaptable and widespread species in Switzerland; it occurs in dense populations in Valais and Ticino and as isolated plants in many low-elevation areas of Switzerland (Figures 1 and 3)
- Other *Opuntia* populations in Bas-Valais, from Martigny to Vouvry, *Cylindropuntia imbricata* in Central Valais, and *O. cespitosa* in Haut-Valais, show little expansion and are therefore not yet invasive. In contrast, *O. mesacantha* and a variant of *O. eneglmanni* may rapidly become invasive in the lake areas of Ticino in well-drained situations. It is advisable to monitor populations in Valais and Ticino to detect any development of certain populations at an early stage.
- We show the importance of taxonomic discrimination between the two species belonging to the *O. humifusa* Complex (*O. mesacantha* and *O. cespitosa*), since their current behavior calls for differentiated management.
- Early mowing encourages the development of creeping Opuntia species. Cutting plants into pieces with wire cutters creates multiple cuttings that can root and make new plants.
- The removal of Opuntias and all other vegetation from the same root space, as is currently practiced, results in a bare soil wasteland, which favors seed germination and the regrowth of even the smallest remnants of cladodes or roots, particularly small creeping species (*O. mesacantha*, *O. cymochila*, *O. fragilis*, *O. polyacantha*).
- For this reason, it is advisable to cut the plants individually at the base, with minimal damage to neighboring native species. This action needs to be repeated regularly, probably for 2–4 years, hence the need to target problem populations and species. However, this approach needs to be tested and refined.

6. Taxonomy of Opuntioideae (Prickly Pears and Chollas) in Southern Switzerland

The species are presented in alphabetical order. For each species, the codes used in Swiss databases and references are indicated (ISFS [27]; Checklist [17]; FloraVS, (https://www.floraVSch/fr/telechargements.html), accessed on 10 January 2025), and the

main references giving good descriptions and photogra)phs are mentioned, with the name used with these references. Phenotypic descriptions are based on observations of plants from Valais, Ticino, and Vaud. Th)ey have been compared with the species and subspecies of their original North American habitat to establish taxonomy. For the *O. humif*usa Complex, we follow the taxonomy established in [28]. The nomenclature used in this article is in line with internationally accepted names from global databases (www.worldfloraonline.org, accessed on 10 January 2025), which also gives the main synonyms used.

In the figure captions, ID numbers refer to georeferenced observations registered in the Info Flora database (Appendix A available from the authors). The dates (day month year) of the photos may differ from the date of the ID observations.

***Cylindropuntia imbricata* (Haw.) F.M. Knuth 1828 (Figure 4)**

ISFS: 128550, Checklist: 1031250, FloraVS: 1787.

References—*Cylindropuntia imbricata* var. *arborescens* (Engelm.) Bulot—[29] (p. 229, pl. 61); *Cylindropuntia imbricata* (Haw.) F.M. Knuth—[5] (p. 209); [8] (p. 32, Figures 20 and 21)—[18] (p. 9, Figures 33 and 34a)—[30] https://www.opuntiads.com/cyl/cylindropuntia-imbricata, accessed on 10 January 2025.

Description.—Shrub or small tree, up to 2 m high and 2 m wide. Elongated cylindrical branches in opposite positions on ascending branches (3- × 10–40 cm). Surface of branches with alternating elongated tubercles giving a braided appearance. Winter appearance, dry with drooping branches. Areoles at apex of tubercles, with numerous (8–20) flattened barbed spines in bundles, cognac to beige in color. Glochids are tiny but well developed on fruit. Flower, 4–5 cm, magenta to fuchsia, with numerous tepals, yellow style, greenish-yellow stigma, dense stamens with yellow anthers. Fruits, 3 × 3 cm, in groups at stem tips, first green, then yellow at maturity, with 8–10 lobes around a deep umbilical depression. Seeds not observed.

Distribution and native habitat—Native to central and northern Mexico, W-Texas, New Mexico, and S-Arizona in sandy or rocky semi-deserts.

Occurrence and habitat in S-Switzerland.—Slow-growing, xero-thermophile plant. Bushes occur isolated or in groups from branches that fell off from a parent plant. The largest colony is at St-Léonard, on a grassy slope above the westernmost quarry, in dolomitic-quartzite rocks. Isolated individuals can be found at Unnru Lichte, Leuk, VS, and at Branson (Grand Champ, Fully, Figures 1 and 2).

Comparison and remarks.—Cold-hardy plant, not very expansive at present, restricted to xeric-microclimatic niches on pH-neutral substrates.

Figure 4. *Cylindropuntia imbricata.* (**a**,**c**) Above quarry east of St-Léonard, VS (ID 12291901, 15 June 2022). (**b**) Unru Lichte, Leuk, VS (ID 16719149, 19 June 24). (**d**) Beneath cross, La Crête des Gardes, St-Léonard, VS (ID 12613083, 9 August 2022).

Cylindropuntia imbricata × *leptocaulis* **(Figure 5)**

ISFS: -, Checklist: -, FloraVS: -.

Description—Shrub, 1 m tall and 1.5 m wide. Shrub made of several steeply rising cylindrical, principal stems (1.5 cm thick) that tend to lignify with age. Youngest portion up to 22 cm long, without branches. Multiple irregularly placed, often curved, cylindrical branches, 1 cm thick, are placed on the principal stems. Stem surface with irregularly placed longitudinal ribs that end sharply upstem, where an areole with one principal and 0–3 shorter spines are placed. Areole, very small, glochids not observed. Spines of cognac to beige color. Flowers presently not observed. Fruits, 1.5 × 1.2 cm in size, often clustered both on stems and stem tips, yellow-orange color in autumn, turning red in winter. Fruits of overall ovoid shape are very tuberculous with an areole and a small spine on some bumps, with 5–6 bumps around a deep umbilical depression. Seeds not observed.

Distribution and native habitat—In comparison, *C. kleiniae* is an established hybrid between these two species with a very large distribution from southern US (New Mexico, Texas) to central Mexico (San Luis Potosí) and southern Hidalgo.

Occurrence and habitat in S-Switzerland.—To date, two individuals grow on the southeastern flank of Tourbillon Hill (Sion).

Comparison and remarks.—This plant is a primary hybrid. Stems are much thinner compared to *C. imbricata*; they have the slightly thicker morphology of *C. leptocaulis*. Its fruit resemble those of *C. imbricata* more but are much smaller. In comparison with *C. imbricata*, the overall habitus is slenderer and smaller, with a more irregular branching style. *C. kleiniae* De Candolle. 1828 has a very similar stem morphology but has smooth ovoid to piriform fruit.

The plants on the Tourbillon hillside have been entered as *C. imbricata* in the Info Flora database. The first mention dates to 2006 [7].

Figure 5. (**a**–**c**) *Cylindropuntia imbricata* × *leptocaulis*, S-slope of Tourbillon Hill, Sion, VS (ID 1735641, 28 December 2024); (**d**) *Echinocereus triglochidiatus* Engelm. The first non-Opuntioideae cactus in Valais, recently discovered by Florian Dessimoz, same locality (ID17356415, 28 December 2024).

Opuntia azurea var. *diplopurpurea* A.M. Powell & Weedin 2004 (Figure 6)

ISFS: -, Checklist: -, FloraVS: -.

References—*Opuntia azurea* Rose—[5] (p. 498); [30] (https://www.opuntiads.com/opuntia-azurea, accessed on 10 January 2025; *Opuntia azurea* var. *diplopurpurea* A.M. Powell & Weedin—[18]: Figure 119.

Description—Small ascending plant. Cladodes, obovate to orbicular, flat, 8 × 10 cm, with a dull, glaucous-green surface. Areoles, pustular, loosely arranged, >2 cm apart, 4–5 per row of the median cladode, distal radial areoles surrounded by purplish hues more intense in winter, 1 cm apart. Radial spines, 4–6 cm long, brownish black, sometimes

associated with a short white one. Rare short spines on the cladode face. Glochids, dark brown, in dense clumps per areole. Flowers with outer tepals, purple-magenta; inner tepals, pale yellow with purplish bases; fruit turning form green to magenta, with scattered glochid-bearing areoles, of which 6–8 are placed around a deep umbilical depression.

Distribution and native habitat—This species is widely distributed, from north–central Mexico to Texas (Big Bend region). It is resistant to low temperatures.

Occurrence and habitat in S-Switzerland—This xero-thermophile species was recently planted in an abandoned vineyard at Tassonnières (Fully).

Figure 6. *Opuntia azurea* var. *diplopurpure*a, Tassonnières, Fully, VS (ID 12694402m (**a**) 14 October 2022; (**b**) 16 July 2024). Size of cladodes, 8 × 10 cm.

Opuntia cymochila Engelm. & J.M. Bigelow 1956 (Figure 7)

ISFS: -, Checklist: -, FloraVS: 1789 (partially).

References—*Opuntia cymochila* Engelm. & J.M. Bigelow—[31] (p. 256, Figures 2 and 7); [5] (p. 494); [16] (p. 6, Figures 13–15); [30] (https://www.opuntiads.com/opuntia-cymochila/, assessed on 10 January 2025); *Opuntia phaeacantha*, Forme 1—[8] (p. 31, Figures 3 and 4); *Opuntia phaeacantha*, Forme 2—[8] (p. 31, Figures 7 and 8); *Opuntia phaeacantha*—[6]: Figure 1.

Description—Creeping plants, only 2 cladodes tall. Orbicular to obovate cladodes, 7–9 × 8–12 cm, with an absinth green surface, wrinkled in winter and during droughts. Wrinkles leave scars on cladodes from previous years. Areoles, densely arranged, 1–2 cm apart, in 6–7 median rows, irregularly aligned. Short spines, present in the distal third of the cladode, in groups of 1–3 per areole, ochre-brown becoming light beige with age. Brownish yellow glochids, in dense clumps per areole. Flowers are lemon-yellow, and distal tepals may be almost translucent, with a more or less apricot-orange-tinged centers. Slightly swollen cylindrical style, greenish to white, greenish-yellow filaments, light-green stigma, white anthers. Fruit clavate, with 10–12 areoles visible on one side, pink to bright red when ripe, and juicy, vermilion-red interior. Seeds of irregular polygonal shape, 4.0–4.7 mm, funicular belt of increasing diameter from 0 to 1.2 mm thick, and bumpy. Cladodes and fruits have a crumpled, dehydrated appearance during winter frosts.

Distribution and native habitat—This species has a wide distribution, from the prairies of the Midwest to Wyoming, Utah, Arizona, Chihuahua, and Texas. It is often the dominant grassland species [31].

Occurrence and habitat in S-Switzerland—This xero-thermophile species thrives on acidic to neutral substrates on gneiss and decalcified loess (pH 6.1–7.1) at Les Follatères, and around Branson (Fully). The rocks at Grand Champ are 60% covered with this creeping species (Figure 2c). In places, it cohabits with *O. mesacantha*. Also present on the south face of Valère Hill (Sion) and in Lavaux, VD (Figure 7a).

Figure 7. *Opuntia cymochila*: (**a**) above St-Saphorin, Lavaux, VD (ID 16461706, 7 June 2024); (**b**,**c**) beneath Grand Champ rock, Branson, Fully, VS (ID 12 748 050): (**b**) 3 June 2003 (ID 12747373), (**c**) 3 February 2023. (**d**) S-wall of Valère Hill, Sion, VS (ID 12660457, 24 September 2022)).

Comparison and remarks.—The author of [8] regarded this species as a variety of *O. phaeacantha*. Consequently, it has been lumped with *O. phaeacantha*. All reference images for *O. paheacantha* of Info Flora (https://www.infoflora.ch/de/flora/opuntia-phaeacantha.html) are in fact *O. cynochila.* Similar lumping is published for Austria [6] (Figure 1).

This species differs from *O. phaeacantha* by cladodes that are more orbicular, smaller, more densely covered with areoles and of a non-glaucous dark green color. In contrast with *O. phaeacantha*, cladodes are wrinkled in winter. The flowers are, in general, of a paler yellow color with less or no (observations in Lavaux) reddish tinge in the center.

This species is invasive at Rocher de Grand Champ (Figure 2c) and along the Chemin des Vignettes, west of Branson (Fully, VS). The recent eradication of adult plants has resulted in the germination of large quantities of seeds and regrowth from cladode or root fragments.

Opuntia engelmannii aggregate (Figures 8–10)

ISFS: -, Checklist: -, FloraVS: 1784.

References—*Opuntia engelmannii* Salm-Dyck ex Engelm.—[5] (p. 497); [8] (p. 32, Figures 13a and 14); [16] (p. 96, Figure 8); [30] (https://www.opuntiads.com/opuntia-engelmannii/); *Opuntia orbiculata* Salm-Dyck ex Pfeiff.—[8] (p. 29, Figures 17–20).

General remarks—Here, we include several morphotaxa (that may represent species, subspecies, varieties) that have been called *O. engelmannii* in the Swiss and European literature [5,8,16,32,33]. These taxa are characterized as spreading and ascending or decumbent shrubs with relatively large (10–20 × 20–20 cm) obovate, spinose cladodes, yellow to orange flowers and juicy, dark red to violet (eggplant colored) ovate to barrel-shaped fruit. At this state of work, rather than attributing a definite North American taxonomy to the various populations, we describe the diversity and the morphologic differences between the forms encountered so far in southern Switzerland. Planned DNA sequencing will hopefully provide insights into genetic relationships in this aggregate. The taxa reported here may have different origins in north America and later in the Mediterranean area, and hence, they have certainly been introduced on several occasions.

***Opuntia* sp. cf. *O. engelmannii* Salm-Dyck ex Pfeiffer (Figure 8c)**

ISFS: -, Checklist: -, FloraVS: 1784.

References—*Opuntia engelmannii* var. *engelmannii*—[29] (p. 171, pl. 44); *Opuntia engelmannii* Salm-Dyck, 1850—[8] (p. 32, Figures 13–14), [6]: Figures 8a–c,e–g.

Description—Ascending plants forming shrubs 1–2 m high and 3–4 m wide. Cladodes, large (up to 20 × 30 cm) and flat (1–2 cm), obovate to broadly obovate, glaucous green. Areoles, loosely arranged, 5–8 in the median diagonal of the cladode. Distal radial areoles, often abundant; 1–3 short (1–2 cm) white spines per areole are found all over the cladode surface but are missing on older cladodes. The abundant glochids are orange-brown, with variable lengths placed in the whole areole, and detach at the slightest touch. Flower, imperial yellow, sometimes with a slight orange tinge in the center. Style, cylindrical, slightly swollen at base, light green. Stigma, medium green; stamens, white. Pericarp with areoles bearing glochids. Fruit the size and shape of a small kiwi, eggplant-colored, with 8–12 areoles visible on one side; juicy interior, sweet, vermilion-red pulp, abundant seeds. Seeds, round, 4–4.5 mm in diameter, funicular belt of variable thickness from 0 to 0.55 mm wide, with numerous small bumps.

Distribution and native habitat—This species is widespread in the US states of Arizona, New Mexico, and Utah and northern Mexico (Chihuahua, Coahuila, Sonora).

Occurrence and habitat in S-Switzerland—*Opuntia* sp. cf. *O. engelmannii* is mainly found in the Fully municipality on rocky gneiss substrates and in dry grasslands with acidic soil (pH 4.9–5.6), facing south or southwest. It is widespread on the rocky slopes and cliffs to the east of Fully, above Saxé and above Mazembroz. Since [2] (p. 32) noted the presence of "four bushes between Mazembroz and Saillon, 500–520 m", this species has gained considerable ground. Thermophilic and very well adapted to drought, it can be found at an altitude of 670 m in the cliffs below Beudon (Fully), and there are dozens of individuals in the cliffs of Les Planches de Mazembre (Figure 2d), most probably propagated from mother plants by birds that eat the sweet, pulpy fruits. It proliferates behind Saxé college (Fully). Recent plantings can be found in Dorénaz, and a few low-vitality plants are present on limestone west of the Saillon (VD) hill. Considered invasive by the Fully municipality, an eradication campaign was undertaken at Les Planches de Mazembre in spring 2023, but small plants are regrowing.

Opuntia sp. cf. *O. engelmannii* occurs also in Lavaux (Bourg-en-Lavaux, VD, ID 16 684 377, 10 June 2024), but this plant may be revealed to be a form of *O. robusta* with further observation.

Comparison and remarks—According to D.J.F., this form looks like *O. orbiculata.* It differs from the closely related species *O. engelmannii* by smaller areoles arranged closer together. On the other hand, glochids are of mixed sites distributed throughout the areole.

Opuntia sp. cf. *O. engelmannii* is invasive in the cliffs of Les Planches E of Mazembroz (Fully).

***Opuntia* sp. cf. *O. engelmannii* var. *flavispina (Benson) Parfitt & Pinkava* (Figure 8a,b,d)**

ISFS: -, Checklist: -, FloraVS: -

References—*Opuntia engelmannii* Salm-Dyck, 1850—[16]: Figure 8d, [30].

Description—Ascending plants forming shrubs 1 m high and 3 m wide. Cladodes (12–20 × 16–28 cm) are flat (1–2 cm), obovate with a strongly tapering base, and olive green. Areoles, small, arranged 5–8 in the median diagonal of the cladode. Distal radial areoles, not abundant. One or two prominent long (4–6 cm) white, flat spines per areole are found all over the cladode surface, and most of them are deflexed and point to the base of the cladode (particularly in winter). Glochids are orange brown, of mixed lengths, reduced on cladode faces but more prominent in distal radial position. Flower, yellow orange, with a well-defined red center. Style, light green. Stigma, medium green; stamens, white. Pericarp with areoles bearing glochids. Ripe fruit, pear-shaped violet, with 2–3 very small areoles visible on one side; juicy interior.

Distribution and native habitat—*O. flavispina* occurs sporadically in southern Arizona and adjacent Mexico [30].

Occurrence and habitat in S-Switzerland—*O.* sp.cf. *O. engelmannii* var. *flavispina* is present only at Les Follatères (Fully) on rocky gneiss substrates and in dry grasslands with acidic soil (pH 4.9–5.6), facing south.

Comparison and remarks—According to D.J.F., this form looks more like a form of *O. orbiculata.* It differs from the closely related species *O. engelmannii* by smaller areoles arranged closer together. On the other hand, glochids are of mixed sites distributed throughout the areole. It differs from *O. engelmannii* var. *flavispina* in having white rather than yellow spines.

Figure 8. (**a**,**b**,**d**) *Opuntia* sp. cf. *O. engelmannii* var. *flavispina*, Les Follatères, Fully, VS (ID 12747421, (**a**,**b**) 20 December 2021, (**d**):23 June 2021); (**c**) *Opuntia* sp. cf. *O. engelmannii*, Les Planches de Mazambre, Fully, VS (ID 12747558, 13 June 2021).

***Opuntia* sp. cf. *O. engelmannii* var. *lindheimeri (Engelm.) B.D.Parfitt & Pinkava* (Figure 9)**

ISFS: -, Checklist: -, FloraVS: -

References.—[5] (p. 498); [30].

Description—Ascending shrub, 1.5 m high; cladodes, large (12–15 × 20 cm), broadly obovate to round, glaucous blue green. Areoles, loosely arranged, 4–5 per diagonal row on cladode face, 4–5 cm apart, somewhat elevated. Spines, scattered, 1–3 per areole with brownish base and white tip; glochids, very short, dark brown. Flowers not observed; fruit, dark magenta, juicy. Leaves, large, curved, abundant on flower buds and young cladodes.

Distribution and native habitat—New Mexico, western and southern Texas, Oklahoma, and southwestern Louisiana [5].

Occurrence and habitat in Switzerland—At present, one plant cultivated in Arbostora, Morcote, TI.

Comparison and remarks—Differs from *O. engelmannii* with a more blue-green color of cladodes and with less, loosely spread areoles per cladode and sparse yellow spines.

Figure 9. *Opuntia* sp. cf. *O. engelmannii* var. *lindheimeri*: (**a**,**b**) garden, Arbostora, Morcote, TI (ID 16172108, 16 May 2024).

***Opuntia* sp. cf. *O. cuija (Griffiths & Hare) Britton & Rose* (Figure 10)**

ISFS:—Checklist: -, FloraVS: -

References.—*Opuntia engelmannii cuija*—[5] (p. 498); *Opuntia engelmannii*—[33–35].

Description—Spreading and ascending or prostrate and hanging plants forming shrubs up to 1 m high and 3 m wide. Cladodes (12–20 × 20–30 cm), broadly obovate, lenticular with a thicker center (in mesic conditions), glaucous green. Areoles, small, black, arranged 7–8 in the median diagonal of the cladode. Distal radial areoles, very dense. One longer (2–4. cm) and zero to two shorter brownish yellow to white flat spines per areole are found all over the cladode but sometimes reduced. Glochids, brownish yellow, sparse and short on cladode face, very prominent and abundant on the upper radial surface of cladode. Flower, greenish yellow, outer tepals with reddish tinge. Pericarp with sparse areoles bearing thin spines. Ripe fruit, cup-shaped violet, with 3–5 small areoles visible on one side; juicy interior.

Distribution and native habitat—Central Mexico,

Occurrence and habitat in S-Switzerland—*Opuntia* sp. cf. *O. cuija* is abundant on the siliceous limestone cliffs near Gandria above Lake Lugano, TI, and occurs on limestone walls in Arbostora, Morcote, TI. It could rapidly expand by bird dispersal along Lake Lugano and Lago Maggiore, where this less cold-hardy plant is now rarely threatened by frost.

Comparison and remarks—Mexican individuals may have spinier fruit and less areoles per cladode. The species has been treated as *O. engelmannii* var. *cuija*. According to D.J.F., this form looks more like a form of *O. orbiculata.*

Figure 10. *Opuntia* sp. cf. *O. cuija*: (**a**,**b**) near Gandria on Lugano Lake, TI (ID 16172109, 16 May 2024); (**c**,**d**) Arbostora, Morcote, TI (ID 16172108, 16 May 2024).

Opuntia ficus-indica (Linnaeus) P. Miller1768 (Figure 11)

ISFS: -, Checklist: -, FloraVS-.

References—Opuntia ficus-indica—[5] (p. 498).

Description—Shrub or small tree, 2–3 m high, with a lignified trunk. Cladodes, obovate to oblong (12–20 × 30 cm), thick (3–4 cm). Areoles, small, elliptical, 5–6 in irregular rows across the cladode; spines, rare, very short, white, or absent. Flowers and fruit not observed at present.

Distribution and native habitat—*O. ficus-indica* is probably native of Mexico [15]. It has been cultivated for its fruit for a long time and has become naturalized in South Africa, Australia, and the Mediterranean. Many horticultural varieties have been developed.

Occurrence and habitat in S-Switzerland—Plants are possibly cultivated in a garden near Cugnaso, TI.

Comparison and remarks—This species is less cold-hardy (−5° C) than the species present in Valais. It is tolerant to humid conditions. It is invasive in many Mediterranean areas. It may become a threat for low-elevation areas of Ticino.

Figure 11. *Opuntia ficus-indica*: (**a**,**b**) garden at Morín, Cugnasco, near Locarno, TI (ID 16172113, 16 May 2024).

Opuntia fragilis (Nutt.) Haw. 1819 (Figure 12)

ISFS: -, Checklist: -, FloraVS: 1785.

References—*Opuntia fragilis* (Nutt.) Haw.—[5] (p. 499); [36] (p. 94, Figures 1–4)—[18] (p. 8, Figures 29–32)—[30] (https://www.opuntiads.com/opuntia-fragilis/, accessed on 10 January 2025).

Description—*O. fragilis* forms dense, spiny clumps that stick to the ground. Cladodes are small (3 × 5–8 cm), dark green, elongated ellipsoidal to cylindrical. Areoles are set on small tubercles, with a white border on young cladodes, made of small glochids that detach at the slightest touch. Distal part of cladodes with a strong brown spine and smaller beige, barbed. Young cladodes disarticulate at the slightest touch and attach themselves to everything, forming zoochore propagules. Flower, pale champagne yellow, tending orange toward the center. Style, yellow; stigma, lime-green with 5 lobes. Filaments, pink to fuchsia red toward the base. Flowering in Valais is earlier than for other species (April–May). The fruit is a dry capsule, generally sterile in Valais.

Distribution and native habitat—*O. fragilis* is the most cold-hardy and northerly species in North America. It prefers sandy or rocky soils on open plains and steppe hills, throughout the NW USA and southern Canada, from Vancouver to the western shores of the Great Lakes [18]. Flowering is often rare and sterile in natural habitats.

Occurrence and habitat in S-Switzerland—This species proliferated with *O. polyacantha* at Les Follatères before it was uprooted at the end of 2021. Young plants are now growing back in this area. It was recently found on the S-foot of Tourbillon Hill (Sion, VS). The presence of *O. fragilis* is inconspicuous and occasional in Valais and has currently no invasive potential.

Comparison and remarks—In the Follatères area, it was found in close association with *O. polyacantha*, also very thorny, but with flat cladodes and fine, white spines.

Figure 12. *Opuntia fragilis*: (**a**,**c**) cultivated above Lausanne, VD, (**a**) 15 December 2024, (**c**) 18 May 2022); (**b**,**d**) Les Follatères, Fully, VS (ID 12747547, (**b**,**d**) 26 August 2021, (**d**) note dried sterile fruit).

Opuntia humifusa (Raf.) Raf. 1830 Complex *sensu* Majure et al. (2017) [28]

ISFS: 279590, Checklist: 1031230, FloraVS: 1786.

References—*Opuntia humifusa* (Raf.) Raf.—[37] (p. 116, Figures 3–6); *Opuntia humifusa* Complex, [28] (p. 9); *Opuntia humifusa* s.l.—[30] (https://www.opuntiads.com/opuntia-humifusa/, accessed on 10 January 2025)

Comparison and remarks—The *Opuntia humifusa* Complex (Majure et al. 2017) [28] is represented in Switzerland by two closely related species [20]), *O. cespitosa* and *O. mesacantha*, previously classified by observers in Info Flora under *O. humifusa* or under *Opuntia* sp. Our observations of this complex are classified under the aggregate *O. humifusa*, with the species listed under "original name". These are the only species with sparse spines and are the most widespread in Switzerland apart from occurrences in the cantons of Valais, Vaud, and Ticino (Figure 1). They also occur in other cantons of Central and Northen Switzerland (GR, LU, NE, SG, and ZH, Figure 3). They tolerate mesic conditions, snow, and a variety of substrates. The species in this complex have been introduced, or even cultivated, for centuries in the vicinity of religious sites, probably as medicinal plants: chapels, crosses, or stations of Ways of the Cross. However, several individuals reported

more than a decade ago as *O. humifusa* have disappeared in Valais from sites with limestone substrata (e.g., Martigny, Vex).

***Opuntia cespitosa* Raf. (1880) (Figure 13)**

FloraVS: ? 1788: *O. macrorhiza* Engelm.

References—Neotype (designated by [38]; *Opuntia cespitosa* Raf.—[37] (p.117, Figures 7–10); [28] (p. 25, Figure 9); [18] (p. 3, Figures 5–8); [30] (https://www.opuntiads.com/opuntia-cespitosa/, accessed on 10 January 2025); *Opuntia macrorhiza* Engelm.—[8] (p. 32, Figures 18 and 19); cf. *O. humifusa* × *phaeacantha*—[8] (p. 34, Figures 22–25).

Description—Sprawling, creeping plant, up to 1 m in diameter. Cladodes, large for the complex, 8–10 × 11–20 cm, obovate, orbicular or spatulate, glossy glabrous surface, olive-green to glaucous, slightly wrinkled in winter. Do not disarticulate. Scattered areoles (4 per median diagonal). Strong, sparse, white spines present on the margin and rarely on the distal surface of cladodes. Brown glochids in straight tufts, 4–6 mm longer than areoles, detachable to the touch. Flower, egg-yellow with orange to red center. Style, rather cylindrical; stigma and filaments, yellow; anthers, white. Fruit, barrel-shaped, dark pink, vermilion-red interior, juicy, round seeds, diameter of 4.2–4.8 mm, smooth funicular girdle, 0.55–0.75 mm wide.

Distribution and native habitat—According to [20], this species is widespread in the Midwestern United States, from the Great Lakes (Ontario, Canada) in the north to Alabama and Mississippi in the south. Its native habitat includes calcareous or sandy rocky sites with *Juniperus* spp. and *Quercus* spp. It tolerates more mesic (more often wet) and grassy conditions than *O. mesacantha*.

Occurrence and habitat in S-Switzerland—*O. cespitosa* is found mainly in the Oberwallis, with rare exceptions at a few sites in Central Valais and Lavaux, VD. Several stations are located in the Naters community, NW of Brig, VS (Figure 1), up to an altitude of 1170 m, and in Ausserberg, VS, up to 1000 m. In the Haut Valais, it is well developed on gneiss or siliceous arenites (St. Anna near St. German, VS) or even carbonate. On the cliffs of Flüe, Varen, VS, it colonizes limestone, favored by wine-growing pomace compost, which lowers the pH of the substrate. It is present on the cliffs near St-Léonard (identified as *O. macrorhiza* in [8]) on quartzo-dolomitic rocks. In the Fully region, there are three exceptions: at Saxon, *O. cespitosa* is found on gneiss (left bank of the Rhone river, less sunny, more humid); above Fully, beside the road to Les Tassonières, *O. cespitosa* is found at the edge of vineyards, in a semi-shaded situation close to forest; at Le Beudonnet, Fully, between 800 and 840 m, the species is found with high vitality on loess. These localities are in the middle of the geographic range of *O. mesacantha*, but *O. cespitosa* grows in local, more mesic conditions. *O. cespitosa* dwells on molasse conglomerates near Lake Léman (Rivaz, Lavaux, VD). Our measurements indicate a soil pH between 4.7 and 7.2 (A1).

Comparison and remarks—This species is not expanding and currently has no invasive potential. *O. cespitosa* differs from *O. mesacantha* in that its cladodes are often twice as large, orbicular or broadly obovate, darker in color and more glaucous. Cladodes do not disarticulate. The egg-yellow flowers have orange to red centers. *O. cespitosa* does not cohabit with *O. mesacantha*.

Figure 13. *Opuntia cespitosa*: (**a**,**d**) dolomite-quartzite rock wall E of St-Leonard, VS (ID 16 719 150, (**a**) 19 June 2024, (**d**) 15 June 2022); (**b**) limestone rock, Flüe, Varan, VS (ID 12678962, 5 October 2022); (**c**) wall of molasse conglomerate, Rivaz Plage, on Lake Léman, VD (ID 12678962, 10 June 2024).

Opuntia mesacantha Raf. 1830 subsp. *mesacantha* (Figure 14)

References.—2017, *Opuntia mesacantha* subsp. *mesacantha*—[28] (p. 48, Figure 13); *Opuntia humifusa* Raf.—[8] (p. 30, Figures 1 and 2); *Opuntia humifusa* s. str.—[18] (p. 3, Figures 1–4).

Description—Creeping plants on rocky substrates, or upright during growth or in lawns. Cladodes, small (2.3–6 × 4.2–11 cm), usually obovate to orbicular in full sun, more elongated elliptical to oblong in partly shaded sites, with a parrot-green glabrous surface, becoming red and wrinkled in winter. Young cladodes disarticulate easily upon contact. Areoles, scattered, in 3–4 in the median diagonal of the cladode, with sparse, strong, white, radial spines, or rarely spineless. Glochids, absent inside areoles; cladodes, often smooth to the touch. Flower, mimosa yellow to imperial yellow, without orange center; swollen cylindrical style, whitish, yellow filaments, white stigma and anthers. Pear-shaped fruit, fuchsia outside and inside, juicy inside. Seeds, 4.1–4.9 mm in diameter, wavy, bumpy funicular girdle, 0.43–0.84 mm wide.

Distribution and native habitat—According to [20], the native habitat of *O. mesacantha* subsp. *mesacantha* extends from the Appalachians to the coastal plains of the eastern USA and northern Mississippi. It occupies dry, sandy to clayey soils on granitic substrates or on stable *Pinus* and *Quercus* hills and dunes in the coastal zone. These soils are often highly acidic, but it tolerates neutral soils. It is threatened in coastal areas of USA [21].

Occurrence and habitat in S-Switzerland—This is the most widespread species in Switzerland. According to images uploaded with observations in Central and Northern Switzerland, most taxa listed as *O. humifusa* correspond to *O. mesacantha*. This species is abundant in Valais between Fully and Sion. It is often found on loess deposits, conglomerates and siliceous sediments (Mont d'Orge, Sion hills, Figure 2b) or on gneiss (Fully). It is scattered as far as Sierre, but it is absent from the Oberwallis. In Chablais, scattered occurrences are found between St-Maurice and Ollon, VD, and in Lavaux, above St-Saphorin, VD. In Ticino, a large population covers a rocky hillside made of gneiss polished b y glacial erosion in Riazzino (Lavertezzo, near Locarno, TI, Figures 1 and 10)

O. mesacantha disappeared or is in the process of disappearing from xeric stations in Valais on limestone listed in the Info Flora database. On the other hand, it shows normal vitality on limestone bedrock in areas with 2–3 times higher anneal rainfall such as in Chabélais and Ticino (see discussion above). Our soil pH measurements indicate values between 6.0 and 7.6 (Figure A1). This species is highly resistant to heat, drought and frost.

Comparison and remarks—*O. mesacantha* subsp. *mesacantha* differs from *O. cespitosa* by cladodes that are halve the size, light green in color, and by flowers that are entirely yellow. It is more thermophilic. *O. mesacantha* subsp. *mesacantha* has found an ideal climate and substrate in Central Valais and Ticino. All the populations observed belong to this subspecies, which is invasive on south-facing slopes and colonizes the thermophilic dry grassland on the hills of Tourbillon, Valère (Figure 2e), and Mont d'Orge (Figures 1 and 2b)).

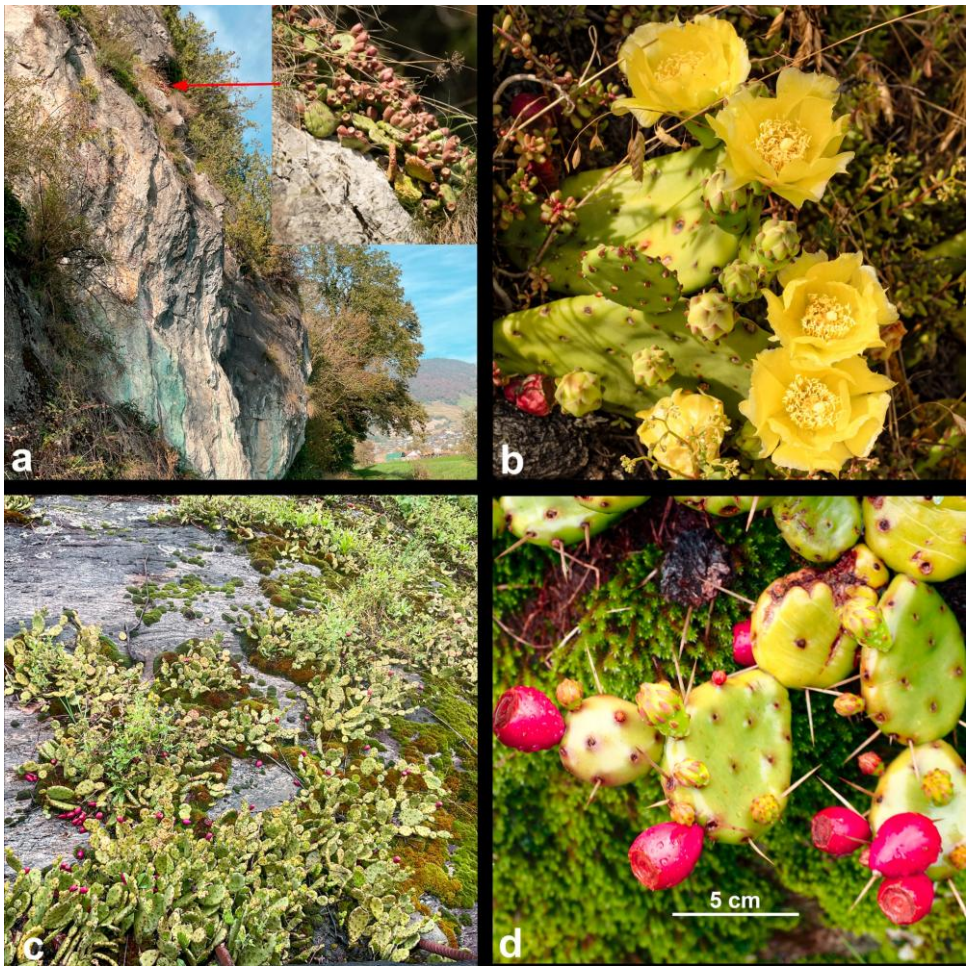

Figure 14. *Opuntia mesacantha*: (**a**) dolomite cliff of St-Triphon near La Pointe, Ollon, VD (ID 17356424, 25 October 2024); (**b**) S-slope of Valère Hill, Sion, VS (ID 15155901, 11 June 2023); (**c**,**d**) proliferation in shallow soil ponds under mesic conditions on glacially eroded gneiss rock, Riazzino, Lavertezzo, TI (ID 16172118, 16 May 2024).

***Opuntia phaeacantha* Engelm. 1849 (Figure 15)**

ISFS: 279810, Checklist: 1031270, FloraVS: 1789 (partially)

References—*Opuntia phaeacantha* Engelm.—[16] (p. 191); [29] (p. 511); [18] (p. 6, Figures 9–12); [30] (https://www.opuntiads.com/opuntia-phaeacantha/, accessed on 10 January 2025); *Opuntia phaeacantha* Engelm. Forme 3, [8] (p. 30, Figures 9 and 10); *Opuntia phaeacantha* Engelm. Forme 1, [8] (p. 31, Figure 6 only); *Opuntia phaeacantha* Engelm. Forme 4, [8] (p. 33, Figure 12 only).

Description—Plants, often upright (50 cm). Elliptical to obovate cladodes (10–15 × 15–20 cm), with a dull, glaucous green surface. Areoles on small bumps, loosely arranged, 2–3 cm apart, 4 to 5 in a diagonal row through the middle of the cladode. Spines, more or less long on the distal ¾ of the cladode, in groups of 2 to 4 per areole, brown to light beige. Reddish-brown glochids in dense, upright tufts per areole. There are two varieties: *O. phaeacantha*, yellow variety, with corn-yellow to orange-yellow flowers with orange-red centers; and *O. phaeacantha*, red variety, with fuchsia-red flowers, often with a reddish tinge around the areoles.

In both varieties, the style is spindle-shaped and light green, as are the filaments. The stigma is green, while the anthers are yellow. The fruit is conical to clavate, pink to red when ripe. Inside, there is a 4–5 mm fibrous wall and a seed-filled capsule in a juicy matrix. Around 6 naked areoles are visible on one side of the fruit. Seeds, 4.2–5 mm in diameter, with strong relief on the concave side. Wavy, bumpy funicular girdle, 0.45 mm wide.

Distribution and native habitat—*O. phaeacantha* is widely distributed in northern Mexico and southwestern USA, from Arizona and Texas in the south to California and Colorado in the north. It prefers sandy to gravelly mineral soils. Its growth form changes according to rainfall.

Occurrence and habitat in S-Switzerland—In Valais, the yellow variety of *O. phaeacantha* occupies the driest, sunniest sites in the Sion hills, notably the southern cliff of Valère and the northeastern end of Tourbillon, where it is very invasive (Figure 2f). It is also invasive on the southern slopes of Mont d'Orge (Sion). *O. phaeacantha* occurs in the Jura Foothills between Eclepens and La Sarraz, VD, on limestone bedrock covered with humus-rich soils. Although this is one of the dryest areas south of the Jura foothills, it receives almost two-fold annual rainfall and much more fog compared to Central Valais.

The red variety is found only under the rocks of Grand Champ and in the gardens of Branson, Fully, VS.

Comparison and remarks—*O. phaeacantha* differs from *O. cymochila* by growing more ascending shrubs, composed of upright branches with several cladodes, which rise above the level of the herbaceous plants in summer. The cladodes are generally more obovate or elliptical than orbicular, larger, glaucous-green in color, and with fewer areoles. Unlike *O. cymochil*a, *O. phaeacantha* cladodes are not wrinkled in winter. The flowers are, in general, of a darker yellow color and have darker orange-red centers.

Opuntia phaeacantha var. yellow is invasive in parts of Tourbillon Hill and Mont d'Orge.

Figure 15. *Opuntia phaeacantha*: (**a**,**c**) yellow variety, Bisse de Mont d'Orge, Sion, VS (ID 16 719 152, 19 June 2024); (**b**) vineyard stone wall at S-foot of Tourbillon Hill, Sion, VS (ID 12748032, 30 September 2021); (**d**) red variety, beneath Grand Champ Rock, Branson, Fully, VS (ID 12747395, 11 June 2023).

Opuntia polyacantha Haw. 1819 (Figures 16 and 17)

ISFS: -, Checklist: -, FloraVS: -

References—*Opuntia polyacantha* Haw.—[29] (p. 221, pl. 58–59); [5] (p. 512); [16] (p. 8, Figures 25–28); [30] https://www.opuntiads.com/opuntia-polyacantha/, accessed on 10 January 2025).

Description—*O. polyacantha* forms dense, very thorny cushions 10 cm high. Cladodes, obovate to spatulate (5 × 8 cm), fleshy. Dense, evenly distributed, pustular areoles with one long spine and several shorter beige ones, pointing toward the base of the cladode. Glochids are very short, light brown. Flower can be colored imperial yellow, champagne-

grapefruit yellow or pink. Style, white or greenish; stigma, light to dark green with 6 lobes; stamens, light yellow. Fruit, very spiny, green becoming beige and dry, very wrinkled, usually sterile. Two varieties can be distinguished: *O. polyacantha* cf. var. *hystricina* (Engelm. & J.M. Bigelow) B.D. Parfitt, very spiny (Figure 16); and *O. polyacantha* var. *juniperina* (Britton & Rose) L.D. Benson, almost thornless (Figure 17).

Distribution and native habitat—*O. polyacantha* has a wide distribution, stretching from northern Mexico to California, the Rockies, the Great Plains and even Canada (Ontario and British Columbia). *O. polyacantha* var. *juniperina* is found in mountainous regions of the Colorado Plateau and southern Rocky Mountains.

Occurrence and habitat in S-Switzerland—Rare plant on crystalline rock (gneiss, greenstone). The species was proliferating, in association with *O. fragilis*, at Les Follatères prior to its removal in late 2021/early 2022. It is also found in Hegdorn (Naters, Valais). *O. polyacantha* var. *juniperina* was only spotted in a rockery above Zeneggen (Valais).

Comparison and remarks—*O. polyacantha* can be distinguished from *O. fragilis* by its flat cladodes and thinner, beige, or even white spines. *O. polyacantha* is very rare in Valais and currently has no invasive potential.

Figure 16. *Opuntia polyacantha* cf. var. *hystricina*. (**a**) Cultivated above Lausanne, VD, origin: Les Follatpres. (**b**–**d**) Les Follatères, Fully, VS ((**b**) ID 12747532, 20 May 2021; (**c**) ID 12747504, 23 June 2021); (**d**) note dry sterile fruit (ID 12 747 541, 26 August 2021)).

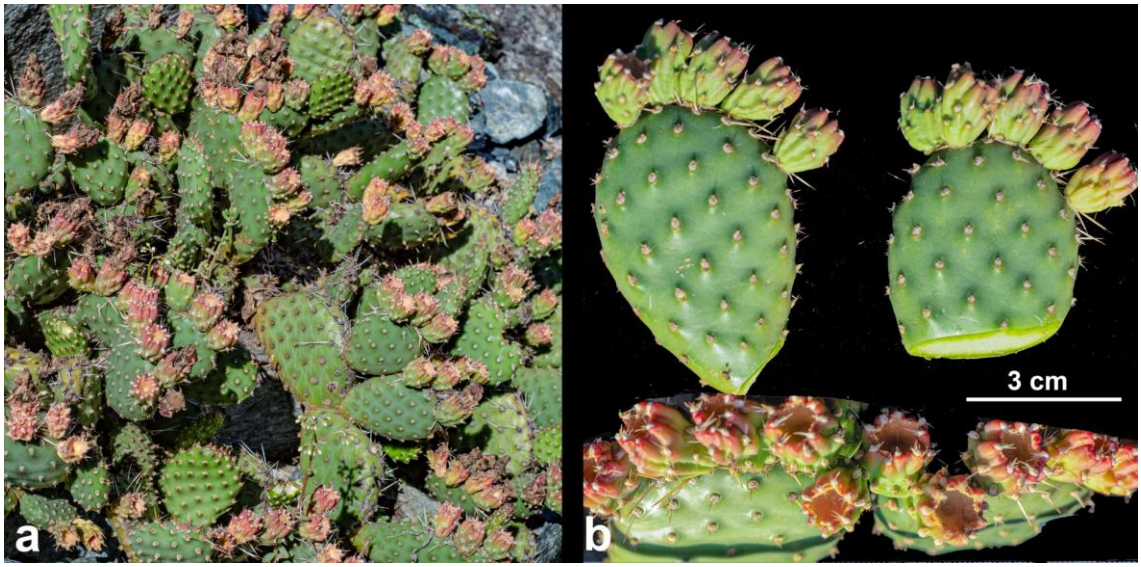

Figure 17. *Opuntia polyacantha* var. *juniperina*: (**a**,**b**) rockery on serpentinite, E of Zeneggen, VS (ID 12296903, 29 September 2022).

***Opuntia scheeri* F.A.C. Weber 1898 (Figure 18)**

ISFS: -, Checklist: -, FloraVS: 1791.

References.—*Opuntia scheeri* F.A.C. Weber—[5] (p. 518); [8] (p. 32, Figures 15 and 16); [16] (p. 7, Figures 21–24).

Description—*O. scheeri* forms ascending shrubs in clusters of 2 m high and 4.5 m wide (western foot of Tourbillon). Cladodes, large (20 × 30 cm), obovate, olive-chartreuse green. Dense, evenly placed areoles with numerous fine, flexible spines arranged in a star shape around the areole. Very fine, orange, brown glochids appear in spring in tufts covering the areoles. Lemon-yellow flowers with numerous tepals. Style, white; stigma, dark green with many lobes. Stamens, pale yellow. Cup-shaped, externally fuchsia-red fruit with a smooth, light-brown umbilical depression. The fruit is covered with numerous areoles with flexible spines, giving it a hairy appearance. The pulp is pink to white. Seeds, polygonal, rounded, 3.9–4.9 mm in diameter, funicular girdle of variable width (0.55–1 mm), with bumps and hollows.

Distribution and native habitat—Central Mexico [5].

Occurrence and habitat in Switzerland.—A thermophile but cold-hardy plant in xeric locations, on siliceous soils. It is currently found only at the western foot of the Tourbillon hill (Sion), after its removal from Les Follatères. The species expands locally but currently has no invasive potential.

Comparison and remarks—*O. scheeri* differs from other large species by the star-shaped arrangement of thin, soft spines around each areole.

Figure 18. *Opuntia scheeri*: (**a**–**c**) SW-foot of Tourbillon Hill, Sion, VS (ID 12660429, 13 June 2021); (**d**) Les Follatères (ID 12747429, 28 August 2021).

Author Contributions: Conceptualization: The aims of this research were initially proposed by P.O.B. and approved by "Service des forêts, de la nature et du paysage du Canton du Valais". Data creation: Data acquisition, edition, and permanent storage was achieved by P.O.B. with the "Online Field-book" of Info Flora (https://fieldbook.infoflora.ch/fr/observations, accessed on 10 January 2025). Funding acquisition: Obtained based on a quote by P.O.B. Investigation: Field work, laboratory work, data acquisition, and data edition were carried out from 2021 to 2024 by POB. Photographic methodology was developed by P.O.B. Validation: D.J.F. and L.C.M. were responsible for the revision and validation of the taxonomy of Opuntioideae presented here. Writing—original draft: preparation of figures including all artwork and photography, P.O.B.; revisions, D.J.F. and L.C.M. All authors have read and agreed to the published version of the manuscript.

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Abbreviations

The following abbreviations are used in this manuscript:

ID	Identification number of each observation in the Info Flora database.
ISFS	« Index synonymique de la flore suisse et territoires limitrophes » (Synonymic index of the flora of Switzerland and adjacent areas) [27].
TI	Canton Ticino.
VD	Canton Vaud.
VS	Canton Valais.

Appendix A

Soil characteristics and pH, Opuntioideae , S-Switzerland

ID Info Flora	locality	municipality	cant.	bedrock	soil color	soil texture	HCl reaction	pH	species, vitality
12289763	Na 1, Bitschji	Naters	VS	gneiss	medium brown	sandy	–	4.7	*O. cespitosa*
12747563	Les Condémines, Mazambre	Fully	VS	gneiss/tillite	medium brown	sandy with pebbles	–	4.9	*O. engelmannii*
12747532	Les Follatères 2, uprooted zone	Fully	VS	gneiss/loess	light brown	mealy	–	5.3	*O. fragilis/polyacantha*
12747421	Follatères "cactus"	Fully	VS	loess	light brown	mealy	–	5.6	*O. engelmannii*
12332298	Branson, Rte des Vignettes Transf.	Fully	VS	gneis/moraine	dark brown	organic soil, sand/pebbles	–	6.1	*O. cymochila*
12300899	hill S of Saint-Clément	Sierre	VS	limestone/loess	yellowish brown	mealy	–	6.1	*O. mesacantha, vit. norm.*
12678996	facing parking Grand Champ Rock	Fully	VS	gneiss/loess	medium brown	mealy	–	6.3	*O. cymochila*
12694418	Champlan in vineyard	Saxon	VS	gneiss/loess	yellowish brown	mealy	–	6.6	*O. cespitosa*
12694404	La Coua, Aproz	Nendaz	VS	tillite	greyish-brown	sandy with pebbles	–	6.7	*O. mesacantha, vit. norm.*
12678962	Flüe	Varen	VS	limestone	dark brown	vine compost	–	7.0	*O. cespitosa*
12764455	Clos des Follatères	Fully	VS	unaltered loess	brownish yellow	mealy	+	7.1	–
12660457	Valère, South cliff	Sion	VS	quartzite	brun foncé	organic soil	–	7.1	*O. cymochila*
12347954	behind Bosch garage	Sion	VS	siliceous calcarenite	dark brown	sandy organic soil	_	7.2	*O. mesacantha, vit. strong*
12613084	Stundhaus	Visperterminen	VS	calcshists	greyish-brown	caclcshist pebbles/sand	+	7.2	*O. cespitosa*
12660461	Les Amandiers	Sion	VS	calcshists	medium brown	sandy with pebbles	+	7.2	*O. mesacantha, vit. weak*
12755199	Batassé-W, behind hut	Sion	VS	limestone	grey	clayey with pebbleas	++	7.2	*O. mesacantha, vit. norm.*
12748068	cliff W of quarry	S. Léonard	VS	dolomite/quartzite	gris brunâtre	clyaey with sand	+	7.3	*O. cespitosa*
12299729	block in vineyard , N of castel	Sierre	VS	limestone	light grey	clayey with pebbles	++	7.4	*O. mesacantha, vit. weak*
12299728	vineyard, Av. des Alpes	Sierre	VS	gypsum	light grey	clayey with pebbles	++	7.6	*O. mesacantha, vit. norm.*
12755199	hill 585 N of Tourbillon	Sion	VS	limestone	dark brown	limy silt with organic nat.	++	7.6	*O. mesacantha absent*
12613083	vineyard Unnru Lichte	Leuk	VS	calcshists	light grey	clayey with pebbles	++	7.8	*C. imbricata*
17356423	Antagne, glacial erratic	Ollon	VD	quartzose conglonerate	dark brown	organic soil	–	6.0	*O. mesacantha, vit. norm.*

Figure A1. Table of soil characteristics and pH in ascending order per canton. ID InfoFløra numbers refer to georeferenced observations registred under this number in the Info Flora database. Toponyms refer to Figures 1 and 2 and the Swiss topographic map (https://map.geo.admin.ch/, accessed on 10 January 2025). pH data are graphically presented in Figure 3a, showing that most Opuntia species prefer acidic to neutral soils but some tolerate slightly alaline soils Alcalimity is caused by the presence of carbonates in the bed rock and the capillary rise in dissolved calcium on hot summer days.

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